
3 1761 04383 7517

AGRICULTURAL AND BIOLOGICAL PUBLICATIONS

CHARLES V. PIPER, CONSULTING EDITOR

BREEDING CROP PLANTS

McGraw-Hill Book Co. Inc.

PUBLISHERS OF BOOKS FOR

Coal Age ▿ Electric Railway Journal
Electrical World ▿ Engineering News-Record
American Machinist ▿ Ingeniería Internacional
Engineering & Mining Journal ▿ Power
Chemical & Metallurgical Engineering
Electrical Merchandising

Digitized by the Internet Archive
in 2007 with funding from
Microsoft Corporation

http://www.archive.org/details/breedingcropplan00hayeuoft



Improved and commercial strains of timothy. At the left, commercial timothy variety, and at the right, one of the improved types produced by Cornell University. (*Courtesy of Myers.*)

(*Frontispiece*)

H

BREEDING CROP PLANTS

BY

HERBERT KENDALL HAYES

PROFESSOR OF PLANT BREEDING, COLLEGE OF AGRICULTURE,
UNIVERSITY OF MINNESOTA

AND

RALPH JOHN GARBER

FORMERLY ASSISTANT PROFESSOR OF PLANT BREEDING, COLLEGE OF AGRICULTURE,
UNIVERSITY OF MINNESOTA; NOW ASSOCIATE PROFESSOR AND HEAD OF
THE DEPARTMENT OF AGRONOMY, UNIVERSITY OF WEST VIRGINIA

FIRST EDITION

164605
8/9/21

McGRAW-HILL BOOK COMPANY, INC.
NEW YORK: 370 SEVENTH AVENUE
LONDON: 6 & 8 BOUVERIE ST., E. C. 4
1921



Copyright, 1921, by the
McGraw-Hill Book Company, Inc.

THE MAPLE PRESS YORK PA

To

Edward Murray East

PREFACE

Since the early development of agriculture by primitive peoples, selection of seed for planting has been an important feature of agricultural practice. While many of our better varieties or strains of crop plants have originated as chance seedlings or from selections made by men who lacked a knowledge of the laws of heredity, there has been a growing appreciation in recent years of the value of training students for the occupation of plant breeding.

Studies in crop genetics carried on since 1900, as well as studies in field plot technic, have helped in a large measure to standardize methods of breeding. Information regarding the mode of inheritance of particular characters as well as a better knowledge of the wild relatives of our crop plants is constantly being obtained. The purpose of this book is to present fundamental principles of crop breeding and to summarize known facts regarding the mode of inheritance of many of the important characters of crop plants. Much of the material here presented has been used in courses in crop breeding which have been given in recent years at the College of Agriculture, University of Minnesota.

Suggestions from others in relation to methods of treatment of various subjects have been of material value. Particular mention should be made of the helpful advice of Dr. M. J. Dorsey regarding the chapters on "Plant Genetics" and "Fruit Breeding;" of F. A. Krantz regarding the chapter on "Potato Breeding," and of John Bushnell and W. T. Tapley regarding the chapter on "Vegetable Breeding."

We are also indebted to Miss Alice McFeely, Bulletin Editor, for many suggestions regarding presentation and for assistance in proofreading; to Mr. A. N. Wilcox for assistance in proofreading; to Miss L. Mae Centerwall for help in obtaining a considerable number of publications from other libraries; and to Miss Alma Schweppe for checking the literature citations. Previous summaries of certain phases of plant breeding methods were

made available through the kindness of Professor Andrew Boss. The many helpful suggestions made by Dr. C. V. Piper, Consulting Editor of these publications have been of great value.

Several illustrations have been supplied by investigators who have made intensive studies of particular crops; credit for these has been given in connection with the illustrations. Most of the other figures are from photographs by T. J. Horton, official photographer at University Farm, St. Paul. Figures on flower structure are from drawings made by G. D. George, illustrator.

The papers of many investigators have been referred to in the text, as the advanced student will frequently desire to study the original publication. The possibilities of errors are very great in a text which reviews the studies of numerous investigators. The writers, therefore, earnestly invite the criticism of the readers.

THE AUTHORS.

UNIVERSITY OF MINNESOTA,
June, 1921.

CONTENTS

CHAPTER I

Introduction

Page

The founders of the art of plant breeding 2
The first demonstration of sex in plants 3
Further proof of plant sexuality 4
The studies of Koelreuter 5
Early studies of the cytology of fertilization 5
An answer to the question of hybrid fertilization 5
The great hybridist Gärtner 6
Early English plant breeders 6
Other workers of this period 7
The relation of certain biologic principles to plant breeding 8
The doctrine of the constancy of species 9
Darwin's theory of natural selection 9
The stability of the germ plasm 10
DeVries' mutation theory 11
The pure-line theory 11
Mendel's law of heredity 12
Hybridization as a means of producing variations 13
The value of crop improvement in relation to a more efficient agriculture 14

CHAPTER II

Plant Genetics

Methods of studying inheritance of characters 16
The mode of sexual reproduction in flowering plants 17
The inheritance factors 20
Variability of characters 20
A cross in which the parents differ by a single factor 22
Inheritance of two independently inherited characters 23
Several factors necessary for the production of a character 25
Linkage of characters in inheritance 26
Inheritance of quantitative characters 27
Stability of inherited factors 32

CHAPTER III

The Mode of Reproduction in Relation to Breeding

Natural crossing with self-fertilized plants 34
Wheat, 34; Barley, Oats, Tobacco, Flax, 36; Rice, 37; Cotton, Grain Sorghums, Peas and Beans, 38; Tomatoes, 39.
The often cross-pollinated plants 39
Maize, Rye, 39; Alfalfa, 40; Grasses, 41.

PAGE
Effects of a cross in normally self-fertilized species 41
Effects of self-fertilization in normally cross-fertilized plants 45
Explanation of hybrid vigor 47

CHAPTER IV

FIELD PLOT TECHNIC

Soil heterogeneity 51
Harris' method of estimating soil heterogeneity 51
Estimating soil heterogeneity by means of checks 53
Use of checks in correcting yields 53
Use of probable error in eliminating strains 57
The pairing method of securing a probable error 57
Replication and its value 58
Size of plot 60
Shape of plot and border effect 61
Competition as a factor in plot variability 62
Climatic variations 64
Summary of field plot technic 65

CHAPTER V

CONTROLLING POLLINATION

Selfing plants artificially 67
Technic of crossing 68
Crossing of smal' grains 69
Crossing large-flowered legumes 71
Depollination with water 73
Summary of technic of crossing 74

CHAPTER VI

CLASSIFICATION AND INHERITANCE IN WHEAT

Genetic classification 75
Wheat species groups 77
Poloni um crossed with other species 79
Some linkage results in wheat crosses 79
Spike density 81
Seed characters 81
Chaff characters 84
Presence or absence of beards 85
Inheritance of disease resistance 85
Inheritance of other characters 87

CHAPTER VII

CLASSIFICATION AND INHERITANCE OF SMALL GRAINS OTHER THAN WHEAT

Classification and inheritance in oats 89
Crosses betwen Avena fatua and A. sativa 90
Origin of cultivated varieties of A. sterilis 90
Differences in awn development 90

PAGE

Color of grain and straw 92
Hulled versus hull-less 93
Pubescence 94
Characters of base of lower grain 94
Open versus side panicle 95
Resistance to rust 95
Size characters 96
Linkage of characters 97
False wild oats 97
Classification and inheritance in barley 98
Species crosses 99
Simple Mendelian characters 102
Winter versus spring habit 103
Density of the spike 103
The barley awn in relation to yield 104
Some rye studies 106
Wheat-rye hybrids 106
Buckwheat 107
Breeding buckwheat 108
Rice 108
Inheritance of characters 108

CHAPTER VIII

METHODS OF BREEDING SMALL GRAINS

Method of keeping continuous records 111
New introductions 113
Selection 114
Summary of methods of selection 115
Crossing 116
Technic of harvesting, thrashing, etc 117

CHAPTER IX

SOME RESULTS OF SELECTION WITH SELF-FERTILIZED CROPS

Early investigators in selection of self-fertilized cereals 118
Selection within a pure line 120
Selection for the purpose of isolating a pure line 125
Wheat selections 128
Oat selections 129
Selections in other self-fertilized crops 131

CHAPTER X

SOME RESULTS OF CROSSING AS A MEANS OF IMPROVING SELF-FERTILIZED CROPS

The improvement of black oats at Svalöf 132
A wheat cross made at Svalöf 134
Wheat breeding at University Farm, Cambridge, England 134
Farrer's wheat breeding in Australia 135

PAGE
Marquis wheat . . . 136
Winter wheat breeding at the Minnesota Experiment Station . . . 137
Breeding beans resistant to Colletotrichum lindemuthianum . . . 139
An improved strain of tobacco . . . 139
Summary . . . 142

CHAPTER XI

COWPEAS, SOYBEANS AND VELVET BEANS

Cowpeas (Vigna sinensis) . . . 143
Origin . . . 143
Description and inheritance . . . 143
Some results of selection and crossing . . . 145
Soybeans (Soja max) . . . 146
Origin . . . 146
Classification and inheritance . . . 146
Breeding . . . 148
Velvet bean (Stizolobium) . . . 149
Origin . . . 149
Important characters and inheritance . . . 149
Mutations . . . 150
Breeding . . . 151

CHAPTER XII

FLAX AND TOBACCO

Flax . . . 153
Species crosses . . . 153
Inter-relation of factors for flower and seed colors . . . 153
Inheritance of size characters . . . 156
Wilt resistance in flax . . . 157
Methods of breeding . . . 158
Tobacco . . . 159
The genus Nicotiana . . . 159
Parthenogenesis . . . 160
Sterility . . . 160
Color characters . . . 161
Quantitative characters . . . 162
Environment as a factor in tobacco breeding . . . 165
Mutations in tobacco . . . 167

CHAPTER XIII

COTTON AND SORGHUM

Cotton . . . 173
Classification and inheritance . . . 173
Mutations in cotton . . . 177
Cotton breeding . . . 177

Page

Sorghum 178
Origin 178
Classification and inheritance 178
Some results of selection 179
Methods of breeding sorghum 179

CHAPTER XIV

Maize Breeding

Origin and species 181
Inheritance of characters 183
Endosperm characters 183
Plant characters 187
Colors in plant organs 187
Podded condition 189
Auricle and ligule 189
Chlorophyll inheritance 190
Some seed and ear characters 192
Size characters 192
Chemica composition 193
Corn improvement by the trained plant breeder 196
Relation of ear characters to yield 197
Ear-to-row breeding 198
Home-grown seed 199
Relation between heterozygosis and vigor 200
Immediate effect of crossing on size of seed 201
F_1 varietal crosses 202
Isolation of homozygous strains 205

CHAPTER XV

Grasses, Clover and Alfalfa

Grasses 207
Breeding timothy 210
Clovers 214
Red clover 214
Selection for disease resistant clover 215
Alfalfa 215
Grimm alfalfa and winter hardiness 216

CHAPTER XVI

Potato Improvement

Origin and species 219
Inheritance 221
Production of new forms 223
The difficulties of obtaining crossed seed 224
Improvement through seedling production 226
Clonal selection 228

CHAPTER XVII

Breeding of Vegetables

Page

Self-fertilized vegetables 234
Origin of vegetables 234
Peas 236
Some classification characters 236
Inheritance 236
Beans 241
Some classification characters 241
Inheritance 242
Tomato 245
Classification characters and inheritance 245
Peppers 246
Classification characters and inheritance 246
Methods of breeding self-fertilized vegetables 247
Cross-fertilized vegetables 248
Radish; origin, inheritance and breeding 249
Beets; inheritance and breeding 250
Cultivated vegetables of the genus Brassica 251
Inheritance 251
Breeding 252
Asparagus; rust resistance 253
Economic Cucurbitaceae 254
Introduction and classification 254
Immediate effect of pollination 256
Cucumber 257
Muskmelon 257
Squashes and gourds 258
Watermelon 258
Breeding Cucurbitaceae 259

CHAPTER XVIII

Fruit Breeding

Origin and antiquity of some fruits 261
Some early studies of fruit improvement 264
Von Mons 264
Knight 264
American pomology 265
Some considerations of fruit breeding 265
Overcoming soil heterogeneity 266
Self-sterility and heterozygosity 267
Inheritance of some characters 271
Apple 271
Raspberry 272
Grape 272
Illustration of methods of breeding 273
Selection of bud sports 273
Controlled crosses 277

CHAPTER XIX

Farmers' Methods of Producing Pure Seeds

Page

Determination of better varieties 281
What is good seed? 282
Adaptability 282
Yielding ability and quality 282
Purity 283
Hardiness 283
Strength of stalk 283
Disease escaping or resistance 283
Methods of seed production 284
Seed growers' methods for self-fertilized crops 284
Improved corn seed 287
Method of breeding corn for special breeders 288
Method of corn breeding for average farmer 290
Potato seed (tubers) selection 290
Improvement by selection of such crops as alfalfa, clover and grasses 292
Seed registry or certification 293
Definitions 294
Literature citations 299
Index 319

BREEDING CROP PLANTS

CHAPTER I

INTRODUCTION

The origin and mode of development of nearly all of our principal cultivated crops is an obscure and much debated subject. This is partly due to the fact that many crops have been grown for hundreds of years and often the same forms are cultivated as were grown in early periods. It is very probable, for example, that the men of the old stone age, 50,000 years ago, had some sort of art of agriculture (Dettweiler, 1914). These conclusions have been drawn from old engravings of this period which were made on cavern walls. Wheat and barley were certainly grown in early times. A carving of the upper Paleolithic age in the Pyrenees mountains shows winter barley such as is now cultivated in that locality.

Dettweiler writes very interestingly of the agriculture of the Lake Dwellers who lived during the period from 4,000 to 2,000 years B.C. He states that the Lake Dwellers of Switzerland cultivated the short-eared, six-rowed barley, *Hordeum sanctum* of the ancients; the dense-eared, six-rowed variety, *H. hexastichon* L., variety *densum;* two-rowed barley, *H. distichon;* small lake-dwelling wheat, *Triticum vulgare antiquorum;* true Binkel wheat, *T. vulgare compactum;* Egyptian or English wheat, *T. turgidum*, L.; an awnless thick-eared emmer, *T. dicoccum*, Schrank; one-grained wheat, *T. monococcum*, L.; meadow (common) millet, *Panicum miliaceum*, L.; club millet, *P. italicum*, L.; and a type of flax, *Linum angustifolium,* which still grows wild in Greece. An excavation was made in the village of Gleichberg, near Romhild in 1906. On an old fireplace, with remains of the oldest Bronze age, were found the following seeds: einkorn, spelt, binkel, and small lake-dwelling wheat, small lake-dwelling barley, vetch, peas, poppy, and possibly apple seeds.

It is not the purpose to give the historical development of crops except to show that many were cultivated in very ancient

times by primitive peoples who developed many varieties. As some of the varieties which were then grown are in existence today and are cultivated in some regions, a little idea of earlier work is obtained.

Coming now more nearly to present times we may briefly consider the work of the Indians with maize. Piper speaks of the plan by which seeds of different colors were planted together in one hill with the thought that this method gave increased yields. It tended to keep the varieties in a heterozygous condition. During the last three or four years Squaw Flint from the Indian reservations in Minnesota has averaged as large a yield per acre at University Farm, St. Paul, as the more carefully selected varieties.

These facts should help to give the student of plant-breeding some idea of the great accomplishments in plant production in earlier times and to correct possible exaggeration of relative values of the results of recent work. Present-day breeding has achieved great results and will accomplish much more; the foundation, however, was laid many years ago.

THE FOUNDERS OF THE ART OF PLANT BREEDING

The relation between the science and the art of plant breeding is a very interesting subject. Through many years of trials, methods are improved; and a correct knowledge of the fundamentals of the science often does not widely modify the actual practice involved. As a rule, scientific principles allow some short cuts in breeding methods and help to eliminate erroneous and useless practices.

As will be constantly emphasized in this work, there is a close relation between the mode of reproduction and the methods of breeding a plant. A knowledge of sexuality was, therefore, almost a necessity before it was possible to develop the art of breeding. Sexual processes, while not thoroughly understood, were observed in animals three or four centuries B.C. by the Egyptians and Assyrians. Existence of fruit-bearing and sterile trees of the date palm was known to the people of Egypt and Mesopotamia in early times and records of artificial pollination as early as 700 years B.C. have been found (see Fig. 1). The Assyrians commonly referred to the date trees as male and female. The Greeks, however, to whom we look for early

scientific thought, failed to interpret this phenomenon. Theophrastus, for example, concludes that as other plants do not as a rule exhibit the same phenomenon, the date tree is *not* an example of real sexuality (Johnson, 1915).

Little was actually known of plant sexual processes until comparatively recent times. The English physician Grew (1676) further developed the suggestion of Sir Thomas Millington that the stamens served as the male organs, by a hypothesis regarding the process of fertilization. The only means of demonstrating this phenomenon was by the experimental method.



FIG. 1.—The date palm among the Assyrians.

"Design from the palace of Sargon at Khorsabad (eighth century B.C.) showing that the male and female flowers of the date palm were clearly distinguished at that time. The worshiper in the middle is carrying a sprig of male or staminate flowers while the one at the right bears female or pistillate blossoms. The drawings should be compared with the photographs of actual flowers. The winged deity at the left, who is usually identified as the Palm God, holds in his hand a cone which is thought to typify the spathe of the male palm, and thus the principle of fertility in general." (*After Johnson*, 1915.)

The First Demonstration of Sex in Plants.—Camerarius first made the experimental test by using isolated female plants of the mulberry, by emasculating the castor bean and by removing the stigmas from Indian corn. The results of these experiments were reported in a letter to Professor Valentin, of Giessen, written in 1694.

The following statement, made by Camerarius and found in Ostwald's Klassiker, page 25, has been frequently quoted (Johnson 1915.)

"In the vegetable kingdom there is accomplished no reproduction by seeds, that most perfect gift of nature, and the usual means of perpetuating the species, unless the previously appearing apices of the flower have already prepared the plant therefor. It appears reasonable to attribute to these anthers a nobler name and the office of male sexual organs."

Further Proof of Plant Sexuality.—The work of Camerarius was confirmed by several men. Thomas Fairchild, in 1719, produced a new variety of pinks by an artificial crossing of two



FIG. 2.—Male and female flowers of date palm about two times natural size. (*Photograph taken by Swingle in Sahara Desert*, 1899.)

varieties; and Bradley, two years earlier, found emasculated tulips set no seed. Miller, 1731, noted insects pollinating emasculated tulips after first visiting untreated tulip flowers. Governor Logan of Pennsylvania, in 1739, experimented with maize and observed that detasseled plants set no seed when isolated from untreated plants. He also removed the silks and found such treated plants were incapable of setting seed. Gleditsch

(1750) had a pistillate palm in Berlin which was 80 years old and had set no seed. He obtained a quantity of pollen from trees in Leipsic (then nine days' journey from Berlin) and after pollination seed was produced which germinated.

The Studies of Koelreuter.[1]—While these investigators and others confirmed the work of Camerarius, little advance was made in the art of breeding until Koelreuter (1761) made a careful study of artificial crosses and gave the first extended account. In tobacco crosses, for example, he found that the first generation was of intermediate habit and therefore showed the effect of the male parent. His work on the vigor of first generation crosses is of much interest. He believed the "oil" of the pollen grain after mixing with the stigmatic fluid penetrated the ovule. The belief of a union of male and female substances was a step in the right direction. The value of insects as carriers of pollen was also demonstrated.

Early Studies in the Cytology of Fertilization.—Pollen tubes were first observed in 1823 by Amici who followed them to the micropyle of the ovule in 1830. Schleiden shortly afterward made numerous studies of the pollen tube and apparently thought the embryo developed in the embryo sac from the end of the pollen tube. This matter was not thoroughly cleared up until Strasburger (see Johnson, 1915) concluded, in 1884, that:

"1. The fertilization process depends upon the copulation with the egg nucleus of the male nucleus which is brought into the egg. 2. The cytoplasm is not concerned in the process. 3. The sperm nucleus, like the egg nucleus, is a true cell nucleus."

An Answer to the Question of Hybrid Fertilization.—Although Koelreuter proved the fact of sexuality in plants it was not generally accepted, and early in the nineteenth century the Physical Section of the Royal Prussian Academy offered a prize for an answer to the question, "Does hybrid fertilization occur in the plant kingdom?" Among other results presented by Weigmann in answer to this question occurs the statement of the immediate effect of pollen in legumes. Weigmann made a study of 36 crosses using the following plants: onion, cabbage, pea, bean, lentil, pink, and tobacco. He observed the fact of variability due to crossing and thought gardeners should pay

[1] For these facts the papers of other writers have been freely used. Those by Roberts (1919) have been especially helpful.

more attention to the planting of their crops so that those of like kind did not grow so near each other that crossing through the aid of insects would take place. Sprengel, in a book published in 1793, showed the important rôle played by insects in pollination and studied the adaptations for crossing found in many flowers. He concluded that nature intended flowers should not be pollinated by their own pollen.

The Great Hybridist Gärtner.—In extent and number of his experiments Gärtner's work is very great. In 1835 he heard of the offer of a prize made by the Dutch Academy of Sciences at Haarlem regarding the place of hybridization in producing new varieties of economic and ornamental plants.

Gärtner's paper on this question, which received the prize, was published in extended form in 1849. He made thousands of crosses, involving nearly 700 species, and obtained about 250 hybrids. The work was so carefully controlled and checked that the fact of sex in plants was thoroughly proved. He made a classification of hybrids according to whether they resembled one or the other parent in all respects, whether they resembled one parent in one part of the plant and the other parent in some other characters, or whether there was an almost equal balance. In the last case in later generations, the inclination toward the one or the other parent was supposed to be due to a slight overbalance of one or the other of the fertilizing materials. Gärtner explains the appearance of the first hybrid generation as due to an inner force operating according to law. He, like Koelreuter and Weigmann, observed increased vigor in hybrids.

He made experiments to determine the immediate effect of pollen with crosses between colorless and colored pericarp varieties of maize and in crosses between a brown-seeded Lychnis and one with a gray seed. As no change occurred, a law was developed to the effect that pollen does not immediately affect forms and external characters of seeds but influences the development of the resultant plant. He observed an immediate effect in some pea crosses and learned that the yellow cotyledon color dominated the green in the hybrid seeds.

Early English Plant Breeders.—Knight, Goss, and Herbert, three English workers, did much to develop the art of breeding. Knight, who was a practical horticulturist, recognized the aid of artificial cross-pollination in producing new kinds. He

studied the question of the immediate effect of pollen. A variety of pea with a white seed-coat was fertilized with pollen of a gray-seeded variety. No immediate influence of pollen was obtained. However, when the resultant plant was pollinated by a white variety both gray- and white-seeded sorts were obtained in the next generation. William Herbert was a contemporary of Knight who learned of the work of Koelreuter some time after he had started his experiments. He opposed the idea that species crosses were necessarily sterile.

Studies made by John Goss are considered of much interest as they showed results similar to those obtained later by Mendel. In 1820 flowers of Blue Prussian pea, which has bluish seeds, were pollinated with pollen of Dwarf Spanish. Three seeds were obtained which were yellowish-white like the male parent. Plants grown from the seeds produced some pods with all blue, some with all white, and some with both blue and white seeds in the same pods. When planted, the blue seeds bred true while the white seeds gave some segregates. No law, however, was developed.

Other Workers of this Period.—At about this same period Sargeret, in France, was making studies with *Cucurbitaceæ* crosses. He observed the fact of dominance as the following crosses show.

Muskmelon (female)	Cantaloupe (male)	First Generation
1. Flesh, white	Flesh, yellow	Flesh, yellow
2. Seeds, white	Seeds, yellow	Seeds, white
3. Skin, smooth	Skin, netted	Skin, netted
4. Ribs, slightly evident	Ribs, strongly pronounced	Ribs, rather pronounced
5. Flavor, sugary and very acid at same time	Flavor, sweet	Flavor, acid

He notes (Roberts, 1919) that:

"The characters were not blended or intermediate at all, but were clearly and distinctly those of the one or the other parent."

Naudin made quite careful studies and attempted to summarize his results. He so nearly approached the law later laid down by Mendel that some workers have spoken of it as the Naudin-Mendel law. He thought that if hybrids were self-fertilized they would return more or less rapidly to the parental types. Similar results were obtained if the hybrid was pollinated

by one of its parents. He noted the uniformity of the first generation and the production of many types in the second generation some of which could not be told from the original parents. The results were explained by the segregation of specific substances in the pollen and ovaries of the hybrid (Naudin, 1865).

Wichura (1865) found reciprocal crosses gave like results and therefore concluded that the pollen and the egg have exactly the same share in the organism which results from fertilization. He studied species crosses in willows but did not deal with the individual characters of the species.

Mendel's work, published in 1866, is now well known to all students of genetics and plant breeding. This early paper remained unnoticed until the rediscovery of the law in 1900 by each of three investigators, DeVries, Correns, and Tschermak. With the great advances made since that time rules can now be given which furnish a reliable guide for plant breeding operations. To quote from Pearl:

"In the creation of new races by hybridization the plant breeder can and does take Mendelian principles as a direct and immediate guide. He has made Mendelism a working tool of his craft."

THE RELATION OF CERTAIN BIOLOGIC PRINCIPLES TO PLANT BREEDING[1]

The art of plant breeding is closely related to those biologic principles which furnish the foundation for the science of breeding. For this reason there is a very close relation between the development of theories of evolution and scientific methods of breeding.

The conception of evolution dates from the time of the Greek philosophers in the eighth century. This was the speculative period and evolutionary beliefs were not attained as a result of experimentation. Until the sciences of botany and zoology were built up it was impossible to do more than outline theories which appealed to the judgment of the writer.

The modern inductive period is of comparatively recent times. Erasmus Darwin developed a theory of evolution which he did not think entirely adequate. Lamarck gave us the first well-rounded theory of evolution. It was based on the inheritance of acquired characters. By continued use an organ was

[1] A bulletin by East (1907) and a book by Scott (1917) have helped materially and have been freely used.

strengthened and developed. Likewise, without use it was weakened. The supposed inheritance of these acquired characters was the basis of the production of the numerous species.

The term species was first applied to animals and plants by John Ray (1628–1705) who used it to refer to a group of organisms with similar characteristics and which freely intercrossed. Many of the experiments of this period dealt with the question of species.

The Doctrine of the Constancy of Species.—Linnæus (1707–1778) adopted a more strict definition although he was not always consistent in his use of the word. The doctrine adopted was that of the separate creation of fixed entities which were called species. Lamarck denied this theory and outlined his evolutionary hypothesis. Most naturalists of this period believed in the immutability of species.

It is thought that the work of Lyell (1797–1875), an eminent geologist, had a marked effect on that of Charles Darwin, who was his intimate friend. Lyell insisted upon the continuity of the earth's history and the uniformity of agencies which wrought such profound changes upon the earth. This theory was in opposition to that of Cuvier, who believed that the earth's history was a series of times of destruction followed by periods of tranquillity ("catastrophism"). After each such destructive period it was believed that new creation took place.

Darwin's Theory of Natural Selection.—The most influential worker in the history of development of the evolutionary conception was Charles Darwin. He and Alfred Russel Wallace independently developed a theory for the origin of species and united in presenting a preliminary paper in 1858.

The publication of Darwin's "Origin of Species" in 1859 gradually brought about a belief in evolution. The work of Lyell had helped materially to develop a belief in the orderly progress of the world and assisted in preparing the way for the masterly presentation of Darwin. Darwin presented such a mass of evidence from widely different fields that the entire thinking world was compelled to accept evolution as a fact. The evidence was grouped under such headings as organic relationship, comparative anatomy, embryology, paleontology, and domestication.

The fact of evolution is indisputable. The explanation is even yet not entirely satisfactory. Darwin's theory is founded upon a series of facts as follows:

1. *Variability.*—It is a matter of common observation that no two individuals are exactly alike. If sufficient individuals are examined the range of variation is found to be quite great. These variations are universally present.

2. *A Struggle for Existence.*—If all the progeny of some of the lower forms grew to maturity and each in turn produced as many progeny, the world would soon be overrun with a single form. There is competition also between different species and genera.

3. *Natural Selection.*—The conclusion would certainly seem reasonable that those forms would survive which possessed characters better adapted to a given environment and therefore gave those particular forms advantage in the struggle for existence.

4. *Heredity.*—Variation produces the material for natural selection to work upon and heredity tends to perpetuate the variations.

The mechanism of transmission of characters, the physiological cause of variations, and the inheritance of different categories of variations were unanswered problems. Many criticisms were made of Darwin's work and many were considered by Darwin himself. Nearly all of these have a bearing upon plant breeding. In the improvement of crops, artificial selection takes the place of natural selection. The breeder is constantly faced with the question of the perpetuation of a variation. He also faces the question of whether the useful variation will perpetuate itself in crosses or will be lost.

Darwin recognized two sorts of variations, the "fortuitous" or chance variations, *i.e.*, those which are everywhere present and which cause every plant to be slightly different from other plants of the same species. These were considered to be of primary importance in evolution. While he recognized "definite" or discontinuous variations, the so-called mutations, these were not considered of primary importance.

The Stability of the Germ Plasm.—Weissmann's theories are of much interest. He developed the idea of the continuity of the germ plasm and that external agencies could not modify inheritance without first affecting the germ cells. Plant breeders are not particularly interested in Weissmann's ingenious theories which were outlined to show that the inheritance of acquired characters was an impossibility. Apparently, in order that a new

character may be produced there must be a modification of the germ plasm. The real question, then, is what causes germinal change? In considering this question we must keep in mind the possibility that agencies which are of little importance from the standpoint of the plant breeder may be of profound importance in evolution.

DeVries' Mutation Theory.—The more recent theory of evolution developed by DeVries attacks the question of the sort of variations which furnish the basis for evolution. DeVries gives only slight value to the small continouus variations and advances the hypothesis that large variations are of primary value. He believes in periods of mutation when from some unknown cause a species is producing many new forms, and other periods when stability of the species is the rule. DeVries recognized three sorts of mutations; (1) progressive, when an entirely new character appears; (2) degressive, the appearance of a partially latent or hidden character; and (3) retrogressive, when an active character becomes latent. The cause, or causes, of these sudden changes was not known. Mutations are frequently not large but small. All sudden heritable changes which cannot be explained by the laws of segregation and recombination are called mutations.

The Pure-line Theory.—The studies of Johannsen are of particular value from the standpoint of the plant breeder. He worked with self-fertilized crops and found that while the progeny of a single self-fertilized plant varied quite widely, these variations were not inherited. From single commercial varieties he found it possible to isolate numerous lines which in their means differed slightly from each other and which bred true. Johannsen considered a pure line to be the progeny of one or more self-fertilizations from a single homozygous ancestor. Selection within such a pure line was of no practical value. Numerous investigations with self-fertilized crops have been made and corroborate the results of Johannsen. Isolated cases of mutations in these pure lines have been reported, and while these are of much scientific interest they occur far too infrequently to be used as a basis for a system of breeding.

Johannsen's pure-line theory has been extended to cover clonal or asexual propagation in both plants and animals. At its proper place evidence will be given to show that in heterozygous organisms which are asexually propagated there sometimes occur

bud sports or somatic mutations each of which may form the basis for a new race. Such bud sports in some plants apparently occur frequently enough to be of economic importance.

Mendel's Law of Heredity.—Mendel's experiments, published in 1866, remained unnoticed until the facts were rediscovered in 1900 by De Vries, by Correns, and by Tschermak. This law furnished the starting point from which the modern study of genetics has developed. Many students will have taken a course in genetics before studying plant breeding. For such students it is sufficient here briefly to review Mendel's law in its application to crop improvement.

Mendel's law can best be understood in relation to cytology. It is well known that the chromosomes are the bearers of the heritable factors. The number of chromosomes for each species is constant and the form and individuality is characteristic. Each chromosome is supposed to be composed of chromomeres and each chromomere may be the seat of a particular inheritable factor. According to Morgan's hypothesis, the factors are located in particular regions of the chromosome. The chromosomes are considered to be in pairs and the two parts of each pair are in such a relation to each other that at reduction division, *i.e.*, at the formation of gametes, the parts of each pair separate and the gamete contains only half as much chromatin as the somatic cell. The gamete then contains one member of each chromosome pair. Exceptions sometimes occur to the above rule when unusual cytologic divisions take place.

A rather recent development of genetics is of primary importance. At some time in preparation for reduction division there is a doubling of the spireme. Morgan supposes that at this time homologous parts of chromosome pairs lie next to each other. These spireme threads wind about each other and in some cases breaks occur. It is then supposed that the chromosomes may reunite in such a manner that a new chromosome is formed which contains parts of each of the homologous chromosomes that make up a pair. If factors are in particular loci this would allow for a different combination of factors in a chromosome containing parts of each chromosome pair.

Most of the previous investigations show that many factors are inherited independently. This allows for numerous combinations when crosses are made. If there is a break, *i.e.*, a crossover or some other means by which factors which are usually

correlated may be recombined, a greater degree of segregation is possible than when factor correlation is absolute.

In general we may say that the number of groups of correlated or partially linked factors is not greater than the number of chromosome pairs. Whether the above explanation is correct, partly so, or entirely wrong, it is a convenient theory with which to account for a large body of facts. It allows for classification of facts in such a way that correct breeding methods may be used.

Mendel's law may then be summarized from the standpoint of the plant breeder as follows:

1. Plants breed true for certain characters when all factors necessary for the development of the character are in a homozygous condition. There is a relative stability of factors. Changes in factors or "mutations" are far too infrequent to furnish a basis for a system of breeding.

2. There is independent segregation of certain factors.

3. Partial coupling of certain determiners sometimes is found. The degree of linkage in transmission is quite constant.

4. Perfect coupling of certain factors occurs, *i.e.*, constant association of characters in inheritance.

As a possible exception to the usual behavior we may mention apparent segregation in the somatic cells of some hybrids. In some forms these changes apparently occur frequently enough to be of practical selective value.

We may summarize Mendel's law in another way by saying that the first generation cross between stable forms may resemble one parent in one character, the other parent in another character or may be intermediate in the character in question. All members[1] of F_1 are of uniform habit. Segregation occurs in F_2 and "segregation of potential characters in the germ cells of hybrids and their chance recombination" (East and Hayes, 1911) may be considered as a general law. In F_3 and later generations some forms breed true, others segregate.

Homozygous forms may be obtained which contain the desirable characters of both parents. Such forms are as stable as races which have been bred by straight selection.

Hybridization as a Means of Producing Variations.—A quite recent explanation for the cause of germinal variation and therefore the main cause of evolution is that of Lotsy (1916),

[1] The meaning of F_1, F_2, etc., and other genetic terms not explained in the text is given in the glossary.

who gives to hybridization the major rôle in the production of variations. Some serious criticisms have been made of this hypothesis as an explanation of evolution. With the higher plants, however, natural crossing has doubtless played an important evolutionary rôle. From the standpoint of the plant breeder crossing is of much importance and it is the *only generally known means of producing variations of selection value that is available as a practical method.* In cross-fertilized species crosses naturally occur followed by segregation, and recombination follows. Selection isolates desirable genotypes.

THE VALUE OF CROP IMPROVEMENT IN RELATION TO A MORE EFFICIENT AGRICULTURE

Maximum yields of crops can be obtained only when all factors relating to the various phases of crop production are favorable. The physical and chemical characteristics of the soil, correct time and rates of planting, and crop rotation must be considered. Recent studies have shown that there are marked differences in the effect of different crops upon those that follow them in the rotation. Of utmost importance is the necessity that the crop be adapted to the soil and climatic conditions in which it is to be grown and that profitable returns be obtained on the basis of the cost of production.

After careful consideration of those factors which go to make up the home of the plant we turn our attention to the seed. The fact that there are remarkable differences in final yields from different varieties of the same crop is commonly known. We are as yet only on the threshold of the possibilities of crop improvement. Careful methods of seed inspection, registration, and treatment to control diseases are necessary to the greatest return from crop breeding. Education of the farmer will do much to overcome the evils of exploitation by the unscrupulous seed dealer or promotor who is anxious only to sell and make a profit on his seed.

The business of growing carefully bred seeds is one that needs an appreciation of these and other factors in seed production. No great amount of special training is needed to carry on this work. To the careful worker who is willing to build up a reputation by actual merit of his seeds, the business of seed production will prove a lucrative one.

The production of improved forms by breeding is a line of work which demands special training. This can be obtained only from a study of the underlying principles of genetics. Nearly all of our land grant colleges and experiment stations, as well as some private seed firms, are carrying on studies in plant breeding. Although these studies are yet in their infancy, results of much value are being obtained. By means of accurate field experiments carried on at research stations and with farmer coöperators, the experiment stations and the federal Department of Agriculture are enabled to give accurate information regarding the better varieties to grow. In the past these studies have not always been made with a correct appreciation of the necessary technic.

It is the purpose of this book to outline methods of breeding in relation to the underlying principles involved, and to present what are coming to be recognized as proper field methods of carrying on these studies. Because the subject is a comparatively recent one, new methods of work are being constantly found. It is therefore necessary to present different viewpoints in order that the prospective breeder may learn why certain practices are giving the better results.

CHAPTER II

PLANT GENETICS[1]

Since the rediscovery of Mendel's law in 1900 there has been an intensive study of the laws of inheritance through experimental breeding and other means. This has resulted in the development of a new biological science which is called Genetics. A knowledge of the principles of this science is a necessity if the student of crop breeding is to pursue his work in the most logical manner. The writers, therefore, believe that a study of genetics should precede plant breeding. There are, however, many people interested in crop improvement who have not had an opportunity to pursue an intensive study of genetics. For this reason it seems advisable to present genetic principles in some detail.

Methods of Studying Inheritance of Characters.—The characters of a plant are those qualities which serve to identify it. They are the means whereby one variety is differentiated from another. The production of a variety with only desirable characters is the main aim of the breeder. It is a commonly accepted fact among geneticists that Mendel's law may be used to explain the inheritance of nearly all plant and animal characters. The character is considered to be the end result of the interaction of certain inherited factors which are located in the germ cells; these factors under favorable environmental conditions cause the production of the character. Thus environment and heredity both play important rôles in character development. The laws of inheritance have been developed mainly by controlled crosses between parents of known inheritance. By correlating the facts of character transmission from parent to offspring with known facts of cytology, an idea of the mechanism of heredity has been obtained. Before presenting a description of the factorial scheme which has been

[1] In preparing this chapter other works on genetics have been freely used. Babcock and Clausen (1918) and East and Jones (1919) have been particularly helpful.

developed to explain Mendelian heredity, it will be necessary to give some of the main facts of reproduction in plants.

The Mode of Sexual Reproduction in Flowering Plants.—Nearly all higher plants produce seeds as the result of the union of sexual cells or gametes. Each body cell which is capable of further division contains a nucleus in which the chromatin is located. This chromatin, which is composed of a definite number of parts or chromosomes, gains its name from the fact that it takes a dark stain with certain reagents when other parts of the

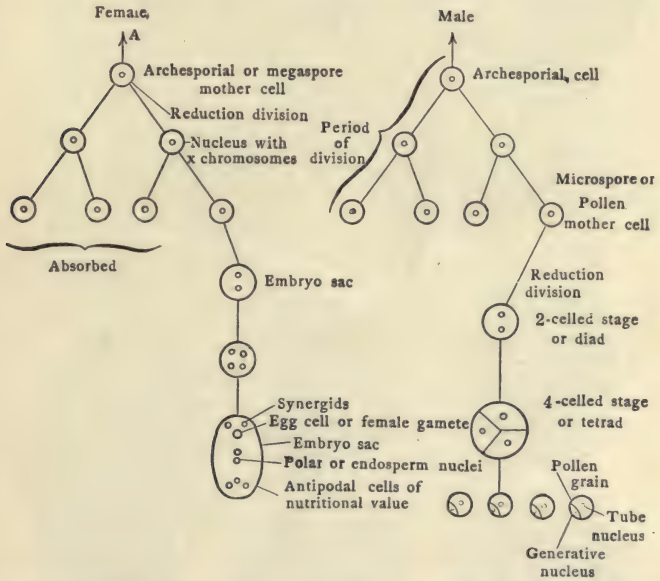


FIG. 3.—Diagram to illustrate production of male and female gametes. A, In some forms as Lilium this megaspore mother cell functions directly as the embryo sac. Reduction division in Lilium occurs at the first nuclear division within the embryo sac.

cell are unstained. In the soma or body of the plant the nucleus of each cell contains a definite number of chromosomes, half of which were obtained from the male sexual cell and half from the egg cell. Each new body cell results from the longitudinal division of the chromosomes of a preceding body cell. Thus all of the somatic cells of a plant contain the same number of chromosomes.

Preparatory to the formation of the germ cells or gametes, the chromosomes assume a paired condition, one member of each

pair being obtained from the male parent and the other from the female parent. At the formation of the sexual cells, or at reduction division, one member of each pair of chromosomes passes to each daughter cell thus reducing the chromosome number to half that in the body cells. Following this reduction division there is an equating division whereby each chromosome is qualitatively

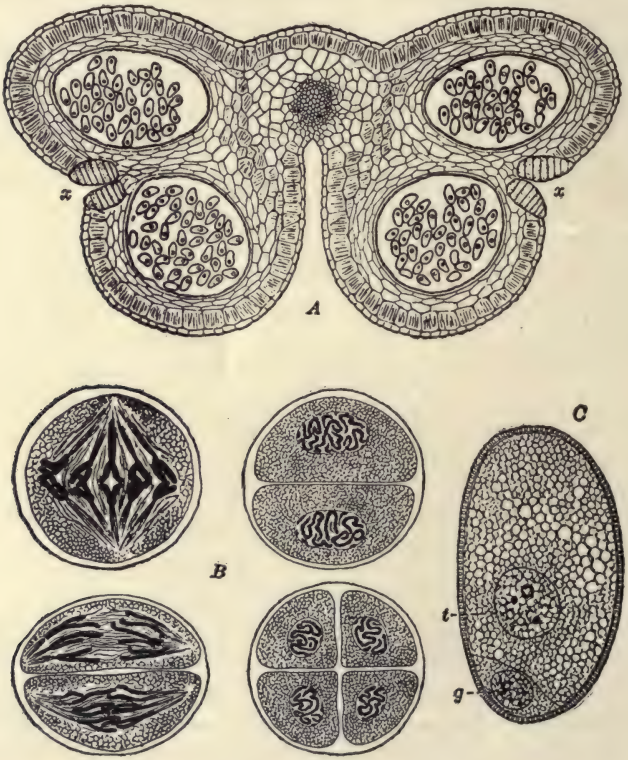


FIG. 4.—Anther and pollen of the lily.

A, Mature anther, showing the four locules, or chambers, containing pollen grains: the anther opens lengthwise on both sides along the lines of cells shown at *x*; *B*, stages in the formation of pollen grains in a group of four (tetrad) within the pollen mother cell; *C*, mature pollen grain with early stages in the development of the male gametophyte; *t*, tube nucleus; *g*, generative nucleus. (*After Bergen and Davis.*)

equally divided. This results in the formation of the male or female sexual cells or gametes as they are called (see Fig. 3).

The male sexual cells are produced in the anthers and are carried in the pollen grains. A mature pollen grain contains two nuclei, a tube nucleus and a generative nucleus (see Fig. 4).

After the pollen grain falls on the pistil the tube cell

elongates, forming a pollen tube which passes down the style. This tube grows through the tissue of the pistil and reaches the embryo sac. The generative nucleus passes into the pollen tube and divides, forming two nuclei which are the male gametes. The pollen tube grows through the tissues of the pistil until it reaches the embryo sac, and the tip of the tube breaks after it penetrates the wall of the embryo sac. In fertilization one of



FIG. 5.—Longitudinal section of the lower portion of the embryo sac of maize at the time of fertilization; *pn*, polar nuclei fusing; *sn*, sperm nucleus fusing with a polar nucleus, *pn*; *e*, egg; *sn*, sperm nucleus in the egg; *pt*, pollen tube; *syn*, synergid; *v*, vacuole. (*After Miller.*)

these gametes of the pollen tube unites with the egg cell to form the embryo of the seed and the other unites with two polar nuclei to form the endosperm (see Fig. 5).

If we represent the chromosome number of each body cell by $2x$, each gamete would be represented by x, the embryo formed by the union of the generative cell with the egg cell would be $2x$ and the endosperm tissue $3x$.

The Inheritance Factors.—The inherited character is considered to be the result of certain definite factors which are located in the chromosome. Moreover, a factor is considered to be located at a certain definite place in the chromosome. After the rediscovery of Mendel's law in 1900, numerous crosses were studied. In many cases the inheritance of each differential character in which the parents differed was easily explained by the hypothesis that one parent contained a genetic factor for the development of the character and that the other parent lacked this factor. This led to the erroneous conception that many characters were dependent on a single factor for their development. That this is not so may be easily seen if one considers that each character is a part of the physiological complex which goes to make up an organism. Thus, many genetic factors play a part in the development of the character. When a cross shows that two parents differ by only a single factor this does not mean that only a single factor is necessary for the development of a character. It does mean, however, that a single factor of inheritance may cause a profound change in the expression of the character of an organism. Some crosses show that many factors play a part in the development of a single character. The present view is that a character is usually the result of the interaction of several factors. When a plant breeds true for a particular character each gamete produced contains all factors necessary for the development of the character. Before considering the results of certain crosses it will be desirable to review briefly the subject of variation.

Variability of Characters.—It is commonly recognized that no two plants or animals are exactly alike. These differences are called variations. Various means of classifying variations have been used. From the standpoint of the plant breeder variations are of two kinds: (1) non-heritable, (2) heritable.

Non-heritable variations are those which are solely due to some difference or differences in the environmental conditions under which the plants develop, while heritable variations are due to some difference or differences in the hereditary characters of the organisms.

Several illustrations may help to make clear what is meant by non-heritable variations. Baur (1914) cites races of *Primula sinensis* which under normal conditions breed constantly true for red and white flowers respectively. If the red race is placed

in partial shade in the greenhouse under temperatures of 30° to 35°C. only white flowers are produced. If those same plants are brought into another greenhouse with temperatures of 15° to 20°C. the flowers which then develop are the normal red color. It is pointed out that what this red primula inherits is not a red flower color but the ability to produce a certain flower color under certain conditions of the environment. Non-inherited variations have no value as a means of producing new varieties or strains. Such variations are, however, of importance to the breeder. For example, a small shriveled seed of wheat has the same inherited characters as a large, plump seed of the same pure line, nevertheless, the seedling produced by the shriveled seed may get an unfavorable start. Familiar examples of non-heritable variations are differences in height of plants, within a variety, which are dependent on differences in food supply, moisture, or sunlight.

Inherited variations may be placed in two classes: (1) mutations, (2) new combinations.

Mutations are due to a sudden change in the hereditary factors of an organism, or to the loss of a genetic factor. In some cases mutations result from abnormal chromosome behavior during the process of cell division. Before we can discuss profitably the reason why mutations occur it will be necessary to know much more about the nature of hereditary factors than we now do. Mutations are sometimes of much value to the breeder. Examples of mutations of economic importance will be found under a discussion of the breeding of various crops. When a desirable mutation occurs it can be utilized as a means of producing a new race. As there is no known means of artificially inducing mutations, the breeder can not depend on them as a means of producing improved varieties.

New combinations result from crossing varieties which contain different hereditary factors. The first generation of a cross between homozygous parents which differ in a certain character may resemble either the one or the other parent or may be intermediated, but all F_1 plants will be of like habit. F_2 plants, however, are of different kinds, due to the segregation of hereditary factors in the germ cells of the F_1 plants. New combinations of factors may occur and thus new individuals may be produced which have some of the characters of the one parent combined with some characters of the other. In some cases characters

which are not present in either parent, appear. These may result from the interaction of two or more factors all of which are necessary for the production of the character and part of which were contained in one parent and part in the other parent. These facts may be illustrated by the results of certain crosses.

A Cross in Which the Parents Differ by a Single Factor.—Sweet corn when mature bears wrinkled seed while flint corn produces smooth seeds filled with starch grains. If sweet corn

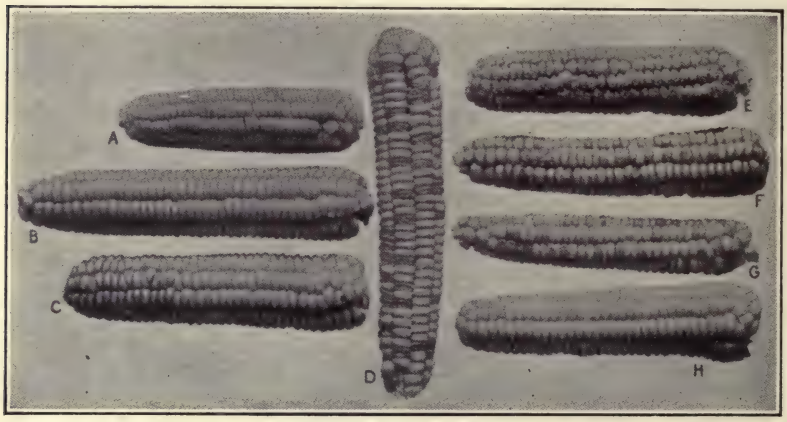


FIG. 6.—Inheritance of starchy and sweet endosperm in maize. *A*, Ear of sweet corn with wrinkled seeds; *C*, ear of flint corn with starchy seeds; *B*, immediate result of pollinating ear of starchy parent with pollen from sweet parent; *D*, produced by self-fertilizing an ear of an F_1 plant of cross between sweet and starchy parent. Note the segregation into sweet and starchy seeds; *E*. An ear produced by planting wrinkled seeds of *D*; *F*, *G*, *H*, ears produced by planting starchy seeds of *D*. Note that one out of every three ears is pure for the starchy character. (*After Babcock and Clausen.*)

is pollinated with pollen from a flint variety the resultant seed is starchy. There is an immediate effect due to double fertilization in which the endosperm results from the union of the polar nuclei with one of the gametes of the pollen grain. If the crossed seeds are planted and the resultant plants self-fertilized, the ears produced will contain starchy and sweet seeds in a 3 : 1 ratio. The facts may be presented by the use of the factor hypothesis. One of the chromosome pairs contains the factors for either the starchy or the sweet condition. Let *S* represent the sweet factor, *F* the starchy factor. In the following diagram only one of the chromosome pairs, which contains the starchy and sweet factors, will be shown.

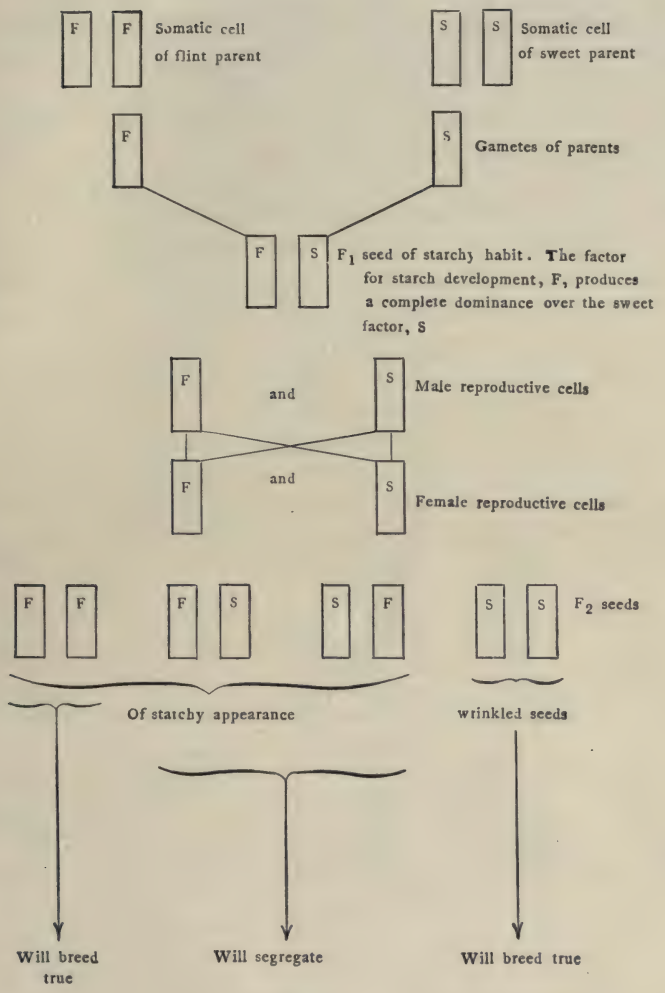


DIAGRAM 1

Inheritance of Two Independently Inherited Characters.—Crosses between varieties which differ in two independently inherited characters may next be illustrated. The parental forms in the case of each differential character will be considered to differ in only a single inherited factor.

PARENTS	CHARACTERS	GAMETES
White Fife wheat	Awnless spike, white seed	*AW*
Preston	Bearded spike, red seed	*BR*

There is a dominance in F_1 of the red seed color (brownish red pigment in one of the bran layers) over the white and a partial dominance of the awnless over the bearded condition. The F_1 plants will therefore, have red seeds and a slight extension of the awns near the top of the spike.

The inherited factors may be considered to be R for red seed, W for white seed, B for bearded, and A for awnless. W and R are considered to be located in homologous loci of one pair of chromosomes and B and A in homologous loci of another pair of chromosomes. The F_1 plants may then be considered as $ABWR$. The gametes of these F_1 plants may contain either A or B in combination with either W or R. The different combinations are supposed to occur in equal frequency.

Wheat (*Triticum vulgare*) has eight pairs of chromosomes. The factors for bearded or awnless spike and for color of seed are independently inherited. Therefore they may be considered to be located in separate chromosome pairs. In the diagram only two chromosome pairs are shown.

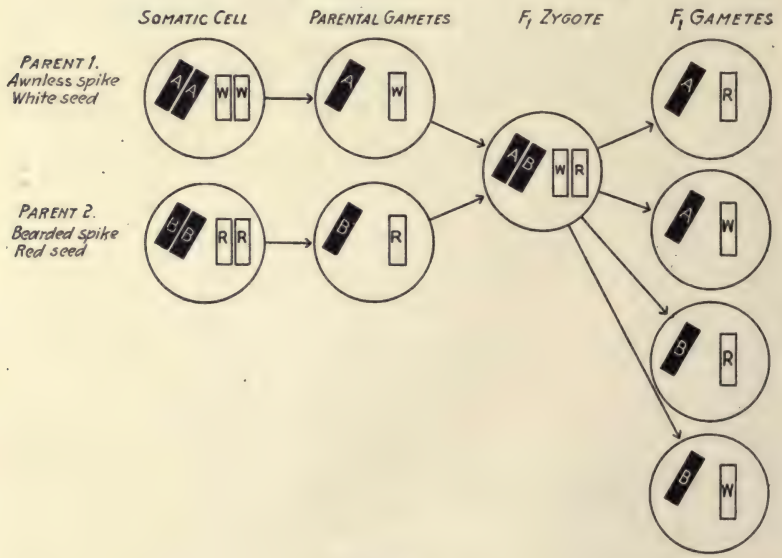


DIAGRAM 2

The F_2 plants obtained by the self-fertilization of F_1 crosses will then be the result of all possible combinations of the gametes. The combination will be illustrated by the Punnet square.

Female gametes	*AR*	*AW*	*BR*	*BW*
	AR	*AW*	*BR*	*BW*
AR	*AR*	*AR*	*AR*	*AR*
	AR	*AW*	*BR*	*BW*
AW	*AW*	*AW*	*AW*	*AW*
	AR	*AW*	*BR*	*BW*
BR	*BR*	*BR*	*BR*	*BR*
	AR	*AW*	*BR*	*BW*
BW	*BW*	*BW*	*BW*	*BW*

Male gametes

Collecting the various combinations we obtain:

	F_2 Plants	F_3 Breeding Habit
1 *AARR*	Awnless, red seed.	Will breed true for awnless spike and red seed.
2 *ABRR*	Int. awns, red seed.	Will segregate for spike character and breed true for red seed.
2 *AARW*	Awnless, red seed.	Will breed true for awnless spike and segregate for seed color.
4 *ABRW*	Int. awns, red seed.	Will segregate for both seed color and spike habit.
1 *AAWW*	Awnless, white seed.	Will breed true for awnless spike and white seed.
2 *ABWW*	Int. awns, red seed.	Will segregate for spike habit and breed true for white seed.
1 *BBRR*	Bearded, red seed.	Will breed true for bearded spike and red seed.
2 *ABRR*	Int. awns, red seed.	Will segregate for spike habit and breed true for red seed.
1 *BBWW*	Bearded, white seed.	Will breed true for bearded spike and white seed.

Several Factors Necessary for the Production of a Character.—In many cases several factors are involved in the production of a single character. Thus the purple aleurone color found in Black Mexican sweet corn is dependent on the interaction of the factors *R*, *C*, *A*, and *Pr* (see Chapter XII, Maize Breeding). *C* and *A* are basic factors both of which must be present for the development of color. When *R*, *C* and *A* are present the color in the aleurone layer is red. Let us study a cross between Black Mexican which is homozygous for purple aleurone color and a white sweet which is homozygous for factors *R* and *A* but which lacks the factors *C*

and *Pr*. The lack of the factor may be represented by a small letter.

Parents	Appearance	Gametes	F_1 cross
Black Mexican.....	Purple color	*PrRAC*	*PrprRRAACc*
White Sweet.....	White color	*prRAc*	

As the F_1 seeds contain all factors necessary for the production of purple color in the aleurone layer, they will be purple. In later generations the factors *R* and *A* may be considered to be present in each gamete, as both parents were homozygous for these characters. The gametes of the F_1 plants will, therefore, be *PrRAC*, *prRAC*, *PrRAc*, and *prRAc*. By the Punnet square method as illustrated in the previous topic, the student may determine the possible F_2 combinations. These will be found to occur in the following proportions:

Combinations	Appearance
1 *PrPrRRAACC* 2 *PrprRRAACC* 2 *PrPrRRAACc* 4 *PrprRRAACc*	9 Purple aleurone
1 *prprRRAACC* 2 *prprRRAACc*	3 Red aleurone
1 *PrPrRRAAcc* 2 *PrprRRAAcc* 1 *prprRRAAcc*	4 White aleurone

Linkage of Characters in Inheritance.—Morgan and his coworkers have made an intensive study of the inheritance of characters in the fruit fly, *Drosophila melanogaster*. Over 300 inherited factors have been studied. If these inherited factors are located in the chromosomes and as there are only four pairs of chromosomes in the fruit fly, it would seem that certain factors should be linked together in their transmission. That this is the case has been clearly proved by the result of many studies.

What frequently happens is that factors which tend to be present in the same chromosome or gamete, sometimes change their linkage relations. That breaks do occur in the chromosomes seems evident from careful cytological studies. Preparatory to reduction division the two chromosomes which make up each each pair lie side by side. There is often a twisting of these chromosomes about each other and in some cases breaks occur and the parts are joined in a new relation which causes a modification of the linkage relation.

The diagram illustrates a change in linkage relations due to a cross-over. *C* and *W* are located in the same chromosome of one parent and *c* and *w* in homologous loci of a similar chromosome of the other parent. If there was perfect linkage the only gametes produced would be *CW* and *cw*. Owing to a cross-over, however, *Cw* and *cW* are also obtained although less frequently

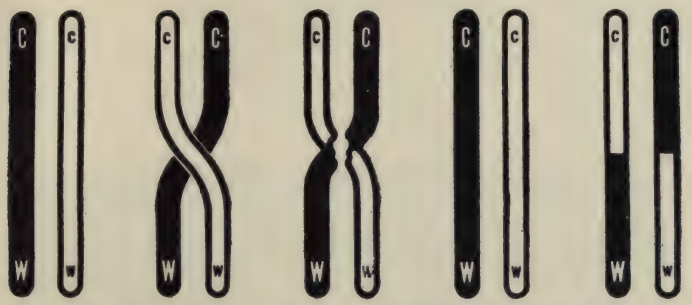


FIG. 7.—Diagrammatic representation of crossing-over and results. At the left, the two original chromosomes. In the middle, the twisted condition of the chromosomes in synapsis and their subsequent separation. At the right, the four types of chromosomes which result. (*After Babcock and Clausen.*)

than the combinations *CW* and *cw*. The following outline expresses the result on a percentage basis:

CW 38.7 per cent.; *cw* 38.7 per cent.	*cW* 11.3 per cent.; *Cw* 11.3 per cent.
non-cross-over gametes	cross-over gametes

Accepting the view that factors are located in particular places in the chromosome, the value of the cross-over hypothesis in explaining degrees of factor linkage becomes apparent. If certain combinations of factors occur with less frequency than others, this means that the breeder must grow a much larger population in the segregating generations in order to obtain the combination desired than when the factors are independently inherited.

Inheritance of Quantitative Characters.—Many of the important characters of economic plants are size or quantitative characters, such as height of plants, size of seed, or relative date of maturity. It was at first thought that these characters did not follow Mendel's law. The discovery that color characters were frequently due to the interaction of several inherited factors led to the explanation of the inheritance of size characters by similar means. Numerous controlled crosses have been studied.

The general nature of the results in this field may be illustrated by a cross between barley varieties which differ in the average length of internodes of the rachis (see Table I).

In this cross between Hanna and Zeocriton, lax and dense varieties respectively, the F_2 ranged from above the modal class of Hanna to the modal class of Zeocriton even though only 141 individuals were studied. The calculated coefficient of variability for the F_2 was three or four times greater than for the parental varieties. Several small F_3 families were grown from F_2 plants representing different densities. By examining the table one will note that some F_3 lines bred comparatively true,



FIG. 8.—Average spikes of the Zeocriton (left), Hanna (right) and four homozygous lines. Mean densities are as follows: Zeocriton, 1.9 mm.; Hanna × Zeocriton, 448–1, 2.3 mm.; 448–5, 2.9 mm.; 448–11–3, 3.7 mm.; 448–16, 4.3 mm.; Hanna, 4.6 mm.

the ranges for density being no greater than for the parental lines and the coefficients of variability also being low. Other F_3 lines were as variable as the F_2 generation while still others were more variable than the parents but less variable than the F_2.

Several F_3 lines, which appeared homozygous, were tested in F_4 and some of these on the basis of the more extensive test again, gave evidence of homozygosity. The general nature of the results is illustrated in Fig. 9. These results show that homozygous lines for density may be obtained in F_3 and F_4, and that in this cross homozygous lines were obtained which approached the densities of the parents as well as homozygous lines with

TABLE I.—HANNA (460) × ZEOCRITON (1039) = 448

Variety	Gen.	Year	Density of parent	Class centers for progeny density in mm.																				Total	Mean	C.V.	
				1.6	1.8	2.0	2.2	2.4	2.6	2.8	3.0	3.2	3.4	3.6	3.8	4.0	4.2	4.4	4.6	4.8	5.0	5.2	5.4	5.6			
Hanna	P_1	1916												6	13	30	10	12	9	2	1				83	4.1±0.02	7.5±0.4
	P_2	1917	3.6–4.9											1	9	39	61	36	20	1					167	4.4±0.01	5.0±0.2
	P_3	1918	4.1–4.7												1	3	26	63	60	36	15	4		1	209	4.6±0.01	5.7±0.2
Zeocriton	P_1	1917			16	18																			34	1.9±0.01	4.8±0.5
	P_2	1918		5	53	72	22	1																	153	2.0±0.01	7.7±0.3
Hybrid 448	F_2	1916				4	8	9	18	18	17	18	12	9	5	13	7	2		1					141	3.0±0.04	23.1±1.0
448–1	F_3	1917	2.1		5	19	18	6																	48	2.1±0.02	8.1±0.6
448–1 (4 pls.)	F_4	1918	1.9–2.4		1	21	85	79	26	1															213	2.3±0.01	7.4±0.2
448–2	F_3	1917	2.4	1	3	17	21	25	6	5	7	4	2												91	2.4±0.03	15.9±0.8
448–5	F_3	1917	2.7					4	16	10	5														35	2.7±0.02	6.3±0.5
448–5 (4 pls.)	F_4	1918	2.7–3.0					3	52	111	104	38	1												309	2.9±0.01	6.6±0.2
448–7	F_3	1917	2.8			2	1		3	13	14	6													39	2.7±0.03	10.2±0.8
448–7–1	F_4	1918	2.0		3	22	56	20	6																107	2.2±0.01	7.7±0.4
448–7–3	F_4	1918	3.1						1	7	42	40	8	4											102	3.1±0.01	5.8±0.3
448–9	F_3	1917	3.0		3	1	4	7	6	7	8	4	1	2	2	1	3								49	2.9±0.06	21.4±1.5
448–9–4	F_4	1918	2.3		6	35	19	3																	63	2.1±0.01	6.8±0.4
448–9–16	F_4	1918	3.2			1	3	1	15	10	8	15	17	6	2	10	7	3	3	3					104	3.3±0.04	19.5±0.9
448–9–19	F_4	1918	3.2								1	5	5	3	1	1									16	3.4±0.04	7.3±0.9
448–9–30	F_4	1918	4.5												1	7	25	14	12						59	4.3±0.02	4.7±0.3
448–11	F_3	1917	3.4							1	6	15	23	8	5										58	3.4±0.02	6.9±0.4
448–11–2	F_4	1918	3.0							11	27	30	4	1											73	3.1±0.01	5.5±0.3
448–11–3	F_4	1918	3.7										5	19	16	5									45	3.7±0.02	4.3±0.3
448–13	F_3	1917	3.5							3	6	12	2	3	12	10	4	1							53	3.6±0.04	12.0±0.8
448–13–1	F_4	1918	3.1							1	9	18	4	6	19	31	24	7	6		1				126	3.8±0.03	12.0±0.5
448–13–2	F_4	1918	3.0							5	13	29	13	4											64	3.2±0.02	6.3±0.4
448–13–5	F_4	1918	4.2												3	21	23	8	1	1					57	4.2±0.02	4.6±0.3
448–16	F_3	1917	4.3												1	3	10	15	8	3					40	4.4±0.02	5.0±0.4
448–16 (4 pls.)	F_4	1918	4.3–4.8											2	11	65	101	77	51	20	3		1		331	4.3±0.01	6.3±0.2
448–18	F_3	1917	4.0								1	3	3	1	2	11	7	5	4		1				38	4.0±0.05	11.2±0.9

intermediate densities. The determination of just how many factors were involved could not be made without a more extensive test. The results can be explained on a genetic basis by the hypothesis that Zeocriton contains three independently inherited factors for density and that Hanna lacks these factors. The added hypothesis may be made that each factor in a heterozygous condition gives half as great an effect as when homozygous. The factors may be considered to have a cumulative effect, two factors when present in a homozygous condition

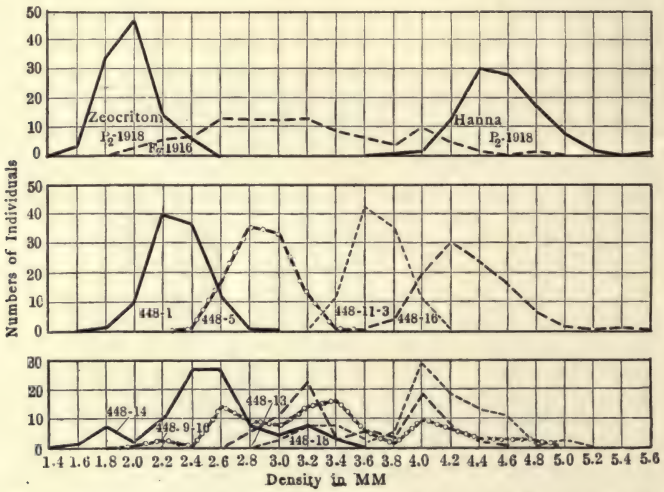


FIG. 9.—Diagrams showing the densities of parental forms and of the F generation in a cross between the Zeocriton and Hanna barleys (upper), of four pure lines (middle), and of several heterozygous lines (lower). (*After Hayes and Harlan*, 1920.)

producing twice as great an effect as when a single factor is homozygous. Other factors of a smaller value are also doubtless present which modify the expression of the main density factors. East and Jones have summarized the results of such controlled crosses and they find a number of general conditions fulfilled.

"1. When pure or homozygous races are crossed, the F_1 populations are similar to the parental races in uniformity. This conclusion devolves from observations that if any particular factors AA and aa are homozygous in the parental races, they can only form Aa individuals in the F_1 generation.

"2. If the parental races are pure, F_2 populations are similar, no matter what F_1 individuals produce them, since all variability in the F_1 generation is the result of varying external conditions.

"3. The variability of the F_2 populations produced from such crosses should be much greater than that of the F_1 populations, and if a sufficient number of individuals are produced the grand-parental types should be recovered. The fulfillment of this condition comes about from the general laws of segregation of factors in F_1 and their recombination in F_2.

"4. In certain cases F_2 individuals should be produced showing a greater or a less extreme development of the character complex than either grandparent. This is merely the result of recombination of modifiers, as was explained above.

"5. Individuals of different types from the F_2 generation should produce populations differing in type. The idea on which this statement is based is, of course, that all F_2 individuals are not alike in their inherited constitution and therefore must breed differently.

"6. Individuals either of the same or of different types chosen from the F_2 generation should give F_3 populations differing in the amount of their variability. This conclusion depends on the fact that some individuals in the F_2 generation will be heterozygous for many factors and some heterozygous for only a few factors."

From the standpoint of the student a hypothetical case may be given to show how the factor hypothesis may be used to explain the inheritance of quantitative characters. Given two barley varieties as follows:

Variety 1, average length of internode of rachis 2.0 mm.
Variety 2, average length of internode of rachis 3.6 mm.

Suppose these varieties differ by two separately inherited factors, *A* and *B*, each when homozygous causing a lengthening of the internode by 0.8 mm.; when heterozygous by 0.4 mm.,

Variety 1 *aabb* Gamete *ab*
Variety 2 *AABB* Gamete *AB* F_1 Zygote *AaBb*

Combinations in F_2 would occur as follows:

F_2 Plants	F_3 Breeding nature
1 *AABB*	Would breed true for length of internode of 3.6 mm.
2 *AaBB*	Would segregate from 3.6 mm. to 2.8 mm.
2 *AABb*	Would segregate from 3.6 mm. to 2.8 mm.
4 *AaBb*	Would segregate as F_2.
1 *AAbb*	Would breed true for length of internode of 2.8 mm.
2 *Aabb*	Would segregate from 2.8 to 2.0 mm.
1 *aaBB*	Would breed true for length of internode of 2.8 mm.
2 *aaBb*	Would segregate from 2.8 to 2.0 mm.
1 *aabb*	Would breed true for length of internode of 2.0 mm.

Probably few size characters are as simple in their inheritance as this illustration. However, the factor notation assists in gaining

a conception of the mode of transmission of these size characters and there seems no good reason for believing that a different mechanism is involved than in the inheritance of color characters. Environmental conditions probably play a larger rôle in the modification of the appearance of size characters than for color characters.

Stability of Inherited Factors.—That sudden changes in the appearance of a character are sometimes found is a well-known fact. The causes of these sudden changes are not so easily determined. Whether these are more logically explained as due to changes in certain inherited factors or due to a new recombination of factors or by other causes is an unanswered question. The pure-line theory of Johannsen was a result of an experimental attack on the question of the stability of a character. A few sudden changes in characters have been observed. Nevertheless, plant characters of self-fertilized crops exhibit remarkable uniformity. Many of the inherited sudden changes which have been noted are most logically explained as the result of a natural cross. Others appear to be due to a sudden change in the hereditary factors of the organism or to the loss of a genetic factor.

The view of factor stability which seems most helpful for the plant breeder has been clearly stated by East and Jones (1919).

"For these and other reasons which might be given, could further space be devoted to the subject, we believe there should be no hesitation in identifying the hypothetical factor unit with the physical unit factor of the germ cells. Occasional changes in the constitution of these factors, changes which may have great or small effects on the characters of the organism, do occur; but their frequency is not such as to make necessary any change in our theory of the factor as a permanent entity. In this conception biology is on a par with chemistry, for the practical usefulness of the conception of stability in the atom is not affected by the knowledge that the atoms of at least one element, radium, are breaking down rapidly enough to make measurement of the process possible."

CHAPTER III

THE MODE OF REPRODUCTION IN RELATION TO BREEDING

General recognition of the stability of inherited factors has served to emphasize the importance of a knowledge of the mode of reproduction of crop plants. If the crop in question is normally self-fertilized, and has been bred carefully, accidental crosses may cause serious mixtures in the variety and thus prohibit its sale as pedigreed seed. With naturally cross-fertilized plants, self-fertilization often has a detrimental effect. A knowledge of the mode of pollination of a crop is therefore an absolute necessity in outlining correct methods of breeding.

As with other characters, environmental conditions play an important rôle. With crops which are adapted for insect pollination and yet which are self-fertile, the number and sort of insects found in the locality may greatly modify the amount of crossing which takes place. Variations in moisture conditions may determine the amount of cross-pollination. The age of the plant also is of importance. Aside from these there are often varietal differences in closely related forms.

Plants may be placed in four groups according to their mode of reproduction. These groups, however, overlap because of prevailing conditions and inherent differences which the plants exhibit.

Group 1.—Naturally self-pollinated: Wheat, oats, barley, peas, beans, flax, tobacco, tomatoes, cotton, sorghums.[1]

Group 2.—Often cross-pollinated: Maize, rye, sugar beets, root crops, grasses, alfalfa, cucurbits.

Group 3.—Cross-pollination obligatory: (*a*) Self-sterile, red clover, sunflower, many fruits; (*b*) Dioecious plants, hops, hemp, asparagus, and date palm.

[1] Some crops, such as sorghum and cotton, cross in the field frequently. As there is no sharp line of demarkation between cross- and self-pollinated plants and as sorghum and cotton should apparently be handled by the breeder in much the same manner as crops like barley, which is seldom naturally cross-pollinated, it seemed wiser to place sorghum and cotton in the self-fertilized group.

Group 4.—Vegetatively propagated: Potatoes, sugar cane, many fruits.

NATURAL CROSSING WITH SELF-FERTILIZED PLANTS

Flower types are adapted for various degrees of self- or cross-fertilization. This in itself is a field in which much study might be made. The plant breeder, however, is chiefly interested in the final result.



FIG. 10.—Natural hybrids in wheat. 1. From right to left: Spike of a pure variety produced from a cross of Turkey winter wheat and Wellman's Fife spring wheat. This is a bearded variety with smooth chaff. The progeny of a single plant of this variety gave 48 bearded, smooth chaffed plants and 2 plants with intermediate (tipped awns) and hairy chaff. 2. From right to left: Preston spring wheat; an F_1 natural hybrid with intermediate awns and hairy chaff. The parental varieties from which these natural hybrids were obtained were grown alternately with Haynes Blue Stem the preceding year.

Wheat.[1]—The individual florets of wheat and barley are much alike. The envelope of a floret of wheat, for example, consists of the flowering glume or lemma and an inner glume or palea. The sexual organs consist of a pistil with a two-branched,

[1] POPE has reviewed much of the literature for cereal crops. See Journ. Amer. Soc. Agron., **8**: 209–227.

feathery stigma and of three stamens with anthers, all of which are enclosed by the lemma and palea. Opposite the base of the palea are two tiny sac-like organs, lodicules. The increase in size of these organs due to water absorption causes the flower to open. This occurs when the stigma is receptive and at this time the elongation of the filaments causes the anthers to protrude from the glumes, when they promptly dehisce. The process of blooming is very rapid and seldom requires more than 20 minutes. Leighty and Hutcheson (1919) state that the opening of the glumes from beginning to completion may not require more than one minute, that the anthers may be extruded and emptied of their contents within two to three minutes and the glumes again become tightly closed at the end of 15 to 20 minutes. Kirchner (1886) states that about one-third of the pollen falls inside the flower. As the pollen is blown around the field by the wind it is easily seen that natural crossing may sometimes occur.



FIG. 11.—Natural wheat-rye hybrids. Two spikes of parent wheat varieties are shown on the outside with hybrid spikes on the inside. (*After Leighty.*)

Investigators differ in their beliefs regarding natural crossing in small grains. De Vries (1906) says "wheat, barley and oats are self-fertile and do not mix in the field through cross-pollination." Biffin (1905) states that he has never observed a case of cross-pollination in wheat; while Fruwirth (1909) lists several German breeders who have given instances of natural crosses. Fruwirth says "wheat varieties can be cultivated side by side for years without mixing." Nilsson-Ehle (1915), in Sweden, has found that some varieties show a much greater amount of natural crossing than others. Howard and others (1910*a*), in India, carefully studied natural crossing in wheat for several years and recorded 231 natural

crosses. Smith (1912) reported eight natural hybrids in 96 rows of Turkey winter wheat and Saunders (1905) told of a natural hybrid which occurred at Ottawa. During the last three years at University Farm, St. Paul, at least 2 to 3 per cent. of natural crossing in wheat has occurred in the plant-breeding plots. Cutler (1919) mentions frequent natural crosses at Saskatoon, Canada.

Barley.—Barley frequently is self-fertilized while the spike is in the sheath. In four-rowed barley the lateral rows overlap in such a way as to form a single row instead of two rows at each edge of the rachis, as in the normal six-rowed varieties. Fruwirth (1909) observed natural crosses in four-rowed barleys and concluded there was practically no crossing in six-rowed forms. He records the observations of Rimpau, who noted only eight suspected natural crosses in barley after growing 40 varieties side by side for a period of eight years. Harlan, after several years' observation at University Farm, Minn. noted only two or three natural crosses. Barley probably, therefore, crosses much less frequently than does wheat.

Oats.—The form of the individual flower of oats is very similar to that of wheat and barley. Tschermak (1901) reports four natural crosses observed by Rimpau, and Fruwirth (1909) records five or six crosses observed by Rimpau after cultivating 19 varieties side by side for eight years. A natural cross between a variety of *Avena sterilis* and *A. nuda* was noted by Pridham in 1916. These facts and numerous statements by breeders as to self-fertilization show that natural crossing occurs much less frequently in oats than in wheat.

Tobacco.—In the tobacco plant the flowers are frequently visited by insects and some natural crossing doubtless takes place. As a rule only one variety of tobacco is grown in a locality. Howard and others (1910 b, c), in India, concluded that there is between 2 and 3 per cent. crossing in tobacco. They emphasize the necessity of producing artificially self-fertilized seed. In breeding experiments, artificially selfed seed is generally used and therefore few records regarding the degree of cross-pollination are available. As it is so easy artificially to self-fertilize tobacco and as each flower produces many seeds (98,910 seeds per plant, Jenkins, 1914) the amount of natural cross-pollination is of little breeding importance.

Flax.—The flax flower, like the tobacco flower, is frequently

visited by insects which may cause natural crossing. Fruwirth (1909) states that crossing seldom takes place. Howard and others (1910a) have observed natural crossing under Indian conditions. Some idea of the frequency of natural crosses may be gained by a determination of the percentage of selected plants which breed true. Results of this nature have been presented by Howard and others (1919).

Year	Number plants selected	Number breeding true
1916	340	334
1917	233	232
1918	232	232

Only 0.9 per cent. of the progeny rows showed segregation.

Rice.—In rice the inflorescence is a terminal panicle of perfect flowers. The one-flowered spikelet has a branched stigma and six stamens. The lodicules are strongly developed. Fruwirth (1909) observed the period of blooming in rice and found that 30 seconds elapsed from the time one flower began to open until it was fully open. Dehiscence of the anthers occurred about seven minutes later and the flower closed three hours afterwards.

In rice self-pollination is the usual method, although opportunities for crossing occur. Hector (1913) thinks crosses may occur at a distance of not more than 2 ft. by the agency of the wind. In lower Bengal 4 per cent. of crossing was estimated. Ikeno (1914) sowed alternate rows of blue- and white-seeded rice. Xenia occurs, blue being dominant, if the white-seeded variety is pollinated by the blue. Fifteen thousand kernels from 190 panicles were examined and no xenia was found. Thompstone (1915), in upper Burma, finds that pollination usually occurs before the glumes open; however, hybrids were frequently observed in fields of ordinary rice. Parnell and others (1918) observed the amount of natural crossing in pure green plants surrounded by others which possessed seed with a purple tip. A total progeny of nearly 15,000 plants grown from seed produced by the green plants were observed, more than 2,000 plants being studied in each of five different families. The percentage of crossing varied from 0.1 per cent. in one variety to 2.9 per cent. in another. Alkemine (1914) states that cross-pollination occurs if the anthers, on account of unfavorable environmental conditions, do not assume their natural position. This happens when the stig-

mas protrude from the glumes and take a pendent position before anther dehiscence takes place.

Cotton.—Probably cotton crosses to a greater extent than any of the other plants, except sorghums, listed as belonging to the naturally self-fertilized group. Because of the difference in observations by investigators it would seem that varietal differences are one probable cause for the discrepancies.

Leake (1911) observed 5 per cent. natural crossing in India. Figures given by Webber (1905) and Balls (1912) range from 5 to 13 per cent.

Grain Sorghums.—Ball (1910) states:

> "All sorghums are adapted to open or wind pollination and most of them are probably adapted to self-fertilization. In adjacent rows of different varieties flowering on approximately the same date, as high as 50 per cent. of the seed produced by the leeward row was found to be cross-pollinated. It is probable that in a fairly uniform field of any given variety a similar percentage of natural crossing takes place."

Graham (1916), in India, made a careful study of the amount of cross-fertilization in the Juar plant (*Andropogon sorghum* Brot.). Crossing was more frequent in the looser types of inflorescence than in the compact types. Single plant cultures were used for the study, which extended over a period of seven years. The percentage of crossing obtained by counting a given number of plants and noting those which were untrue to type gave 97 plants out of 1,577 (6 per cent.) in the loose headed type and only two plants out of 292 (0.6 per cent.) in the compact type of panicle. Preliminary studies were made by Karper and Conner (1919) of the amount of cross-pollination in plants of white milo which were found growing in a plot of yellow milo. The yellow and white varieties flowered simultaneously. Forty-one heads of white milo, which had been surrounded by yellow milo, were planted the following year. An average of 6 per cent. of natural crossing in plants so surrounded was noted.

Peas and Beans.—Piper (1912) finds that natural crossing in the cowpea occurs but rarely in most localities. At Arlington Farm, in the experimental plots, instances of natural crossing have been observed. In some instances natural crossing occurs more frequently. Thus an Indiana farmer, who originally grew only eight varieties, found after several years that he had over 40 types. The new types, Piper concluded, were the result of

natural crosses. Similar crosses have been observed at the Michigan station. Harland (1919) has recorded a supposed case of a natural cross which occurred in one of his hybrid cowpea families.

Natural hybrids of soybeans have been observed at the United States experimental farm in Virginia and also at the Kansas experiment station (Piper 1916). They were detected by the peculiar color of their seed. Varieties of soybeans were interplanted at the Wisconsin station and the amount of natural crossing was determined by testing the progeny. More than 10,000 plants were tested and only a fraction of 1 per cent. of natural crossing was found (Russell and Morrison, 1919).

Although horticultural peas and beans are largely self-pollinated, cross-pollination does occasionally occur. Howard and others (1910a) give observations in India which indicate natural crosses both in garden and field peas.

Tomatoes.—Jones (1916) planted alternate plants of dwarf and standard varieties of tomatoes 3 ft. apart in a field. Seed from the dwarfs was tested the following year. As standard habit is a dominant character, pollen from a standard plant fertilizing a dwarf would give a standard in F_1.

A total of 2,170 plants were grown from seed of dwarfs and 43 proved to be standards. This is practically 2 per cent. As there was nearly as great opportunity for dwarfs to be crossed with dwarf pollen it would seem that between 3 and 4 per cent. of crossing occurred in this experiment.

THE OFTEN CROSS-POLLINATED PLANTS

Maize.—Maize has been placed at the head of the often cross-pollinated group, as crossing is its normal form of reproduction. Fruwirth (1909) found a setting of 24 per cent. in unenclosed corn plants when far enough from other plants to prevent crossing. Knuth (1909), in similar experiments, found 16 per cent. selfing on the upper ear and 4 per cent. on the lower. Preliminary experiments have been made by planting corn with a recessive endosperm color in a field of a variety with a dominant endosperm character. Self-fertilization in these experiments was probably less than 5 per cent. (Waller, 1917, Hayes, 1918*b*).

Rye.—The flowers of rye are very similar to those of wheat and barley. According to Hildebrand the anthers project

between the partly closed glumes until the bases protrude. They then tip over and dehisce, spilling part of the pollen outside the flower. Being lower than the stigma the pollen can not reach the stigma of the same flower. There is some evidence (Ulrich, 1902) (Fruwirth, 1909) which indicates that the rye flower is self-sterile, but that the spikelet is not necessarily so. Further studies are needed to clear up this point.

Ulrich (1902) found significant differences between varieties and individuals of the same variety in the amount of self-sterility. The following table shows some of his results, obtained from artificial and natural pollination. Artificial pollination was obtained by covering the head with double paper bags.

TABLE II.—SELF-STERILITY IN RYE

Variety	Artificial pollination			Natural pollination, per cent.
	Individual spikes, per cent.	Groups of more than 1 spike		
		Same plant, per cent.	Dif. plant, per cent.	
Petkuser	1.30	2.52	28.29	80
Probsteier	2.33	4.98	25.12	59
Schlanstedter	5.02	7.21	38.32	78

Heribert Nilsson (1916) isolated lines in Petkuser rye differing greatly in amount of self-sterility. Of 73 plant selections, 71 were practically self-sterile, one showed segregation, and one proved to be highly self-fertile. The rye flower is probably largely cross-pollinated and because of the heterozygous condition, strains differing in fertility make up any particular variety.

Alfalfa.—Piper and others (1914) working with alfalfa have found about the same percentages of seed set when a flower was self-pollinated as when it was crossed with pollen from flowers on the same plant. When cross-pollination was practiced, approximately 50 per cent. more seed was obtained than from self-fertilization. They also found that pollen of *Medicago falcata* was as efficient in fertilizing *M. sativa* as pollen from other *sativa* plants.

Waldron (1919), in North Dakota, planted together in equal numbers two species of *Medicago*, *sativa* and *falcata*. Seeds from each of the species were planted the following year and the number of hybrids noted. From *M. falcata* 42.7 per cent. of

hybrid plants were obtained and from the *M. sativa* seed about 7.5 per cent. A part of the difference in the results is doubtless due to the fact that the plants produce a smaller number of flowers and are procumbent to prostrate in habit. To find the amount of cross-pollination that normally occurs in alfalfa, one might average the above results and multiply the result by two. This gives in the neighborhood of 50 per cent. of natural crossing which is only indicative of the probable amount.

Grasses.—Some studies with grasses have been reported by Frandsen (1917). Results obtained are given in the following table. Some sterility is indicated by comparing the results of self-fertilization with those of cross-fertilization and natural pollination. *Poa fertilis* and *Bromus arvensis* appear self-fertile. Considerable self-sterility is indicated in orchard grass, timothy, and fescue.

TABLE III.—POLLINATION OF GRASSES

Common name	Scientific name	Percentage seed setting		
		Self-fertilizing	Cross-fertilizing	Free-flowering
Orchard	*Dactylis glomerata*	1.3–11.5	4.3–75.8	50.0
Tall meadow oat	*Arrhenatherum elatius*	5.4–9.4	47.9	51.0
Fescue	*Festuca pratensis*	3.6–9.2	17.8–54.0	35.2–47.7
Meadow foxtail	*Alopecurus pratensis*	7.0–23.3	29.0–69.5	73.2
Italian rye	*Lolium multiflorum*	10.3		79.8
Timothy	*Phleum pratensis*	0.8– 8.5	52.0	91.3
	Poa fertilis	59.7–66.8	63.5–65.5	70.4
Brome	*Bromus arvensis*	66.6–80.0	80.4	77.2–89.2

EFFECTS OF A CROSS IN NORMALLY SELF-FERTILIZED SPECIES

A cross between closely related varieties frequently exhibits a quite marked increase in vigor when compared with the parents. This is a manifestation of the same phenomenon as decrease in vigor which is commonly the result of self-fertilizing a naturally cross-fertilized species. With self-fertilized crops it is usually not possible to utilize this increased vigor because the cost of producing crossed seed is too great. Examples of F_1 crosses in tomato, tobacco, and wheat will be given.

Table IV gives the comparative yields of first generation

tobacco crosses and their parents. All crosses do not prove equally vigorous and a few give no increase as compared with the parental average. In general, however, the crosses show increased yields. As the tobacco flower produces many seeds, Houser (1912) believes the extra cost of production would not be prohibitive. Before this plan can be adopted commercially, extensive studies are needed to determine the value of particular F_1 tobacco crosses.

TABLE IV.—RELATION OF YIELD PER ACRE BETWEEN FIRST GENERATION HYBRID TOBACCO AND THE PARENT PLANTS

Average yield of parents, lb.	Average increase of hybrid over parents, lb.	Maximum increase of hybrid over parents, lb.
800– 900	260	485
901–1,000	212	464
1,001–1,100	185	354
1,101–1,200	153	315
1,201–1,300	153	285
1,301–1,400	159	239
over 1,400	156	189
Difference in yield of parents		
1–100	197	485
101–200	131	181
201–300	189	260
301–400	97	360
401–500	164	215
over 500	175	465

The vigor of F_1 tomato crosses has received some study. The first extensive test was made by Wellington (1912) at the Geneva (New York) Station. A 3-year test was made under field conditions of a cross between Dwarf Aristocrat, a dwarf tomato, and Livingston Stone. Yields of the parents, the F_1, and the F_2 generations are given.

We are not so much interested at the present time in the commercial value of such crosses as in the development of the principle involved. Wellington believes the above cross of sufficient value to more than pay for the cost of producing crossed seed.

Similar results were obtained at the Connecticut Station in a cross between Stone and Dwarf Champion tomatoes. The

TABLE V.—YIELDS OF FRUIT IN THE F_1 AND F_2 GENERATIONS OF A CROSS BETWEEN DWARF ARISTOCRAT AND LIVINGSTON STONE WITH THE PARENTS

Data taken	Year	Dwarf Aristocrat, lb.	Livingston Stone, lb.	F_1, lb.	F_2, lb.
Ripe fruit per plant.....	1908	8.5	12.3	13.9	
Ripe fruit per plant.....	1909	6.1	10.1	12.9	12.0
Ripe fruit per plant.....	1910	7.0	12.0	13.2	10.0
Average.....		7.2	11.5	13.3	11.0
Total fruit per plant.....	1908	14.8	20.9	25.3	
Total fruit per plant.....	1909	9.7	17.7	20.0	20.0
Total fruit per plant.....	1910	14.8	24.7	27.7	25.1
Average.....		13.1	21.1	24.3	22.6

experiment was carried on for four years (Hayes and Jones, 1916). The lowest increase in yield over the better parent was 11 per cent. and the highest 17 per cent. The cross averaged 15 per cent. more fruit by weight than the better parent.

In average weight of fruit the cross exceeded the parental average by 8 per cent. It approached the fruit number of the Dwarf Champion parent and exceeded the average fruit number of the parents by 8 per cent. The cross also matured somewhat earlier than the early parent. A cross between the standard varieties, Lorillard and Best of All, was also studied. The parents produced about the same average size and weight of fruit and the cross about the same as the parents.

A determination of the comparative vigor of F_1 wheat crosses and their parents was made by Fred Griffee, a graduate student in plant breeding at the University of Minnesota. For this purpose pure lines of *T. durum*, *T. dicoccum* and *T. compactum* were crossed with pure line varieties of *T. vulgare*. Intervarietal crosses between pure lines of *T. vulgare* were also studied, as well as crosses between *T. compactum* with *T. durum* and *T. dicoccum*.

A determination of the immediate effect of foreign pollen on size of seed was made. Parental plants were emasculated and then some of the spikes were artificially pollinated with pollen from other plants of the same pure line (incrossed seed) and in another series spikes were pollinated with pollen from another variety or species (crossed seed). Only those crosses were compared in which the average date of pollination was about the

same for the incrossed and crossed seed. Results are presented in Table VI.

TABLE VI.—WEIGHT OF SEED OF INCROSSED PARENTS COMPARED WITH WEIGHT OF THE IMMEDIATE CROSS

Name of cross	♀ Parent		Cross		Difference cross–female parent
	No. seeds	Average weight seed, mg.	No. seeds	Average weight seed, mg.	
Marquis × Velvet Chaff	38	12.6±0.5	48	15.6±0.5	+3.0±0.7
Marquis × Penny	38	12.6±0.5	24	20.2±1.0	+7.6±1.1
Haynes Bluestem × Marquis	49	17.2±0.8	26	23.5±0.7	+6.3±1.1
Little Club × Marquis	39	10.1±0.5	50	9.4±0.3	−0.7±0.6
Emmer × Velvet Chaff	44	26.4±0.8	24	27.1±1.3	+0.7±1.5
Velvet Chaff × Mindum	104	19.9±0.6	23	15.9±0.6	−4.0±0.8
Emmer × Little Club	44	26.4±0.8	15	25.0±1.2	−1.4±1.4

All three crosses between varieties of *T. vulgare* gave increases over incrossed seed. These appear significant in relation to the computed probable errors. Of the crosses between wheat species only one gave a difference which appears at all significant. In the cross between Velvet Chaff and Mindum the incrossed seed seems somewhat heavier in the light of the probable error than the crossed seed. These results show an immediate effect of pollination on seed size in crosses between varieties of *T. vulgare*.

The emasculation and artificial pollination causes a reduction in seed size as compared with normally produced seed. Incrossed, normally produced seed and crossed seed were grown in the greenhouse under controlled conditions and the comparative vigor of parents and crosses was determined. As there were no significant correlations between size of seed planted (even when incrossed seed was compared with normal seed) and resultant plant vigor, the differences between the parents and crosses may be explained on the basis of inheritance.

Average yield of plants in grams of seed will be used as a measure of vigor (see Table VII).

The crosses between varieties of *T. vulgare* and the crosses between *T. vulgare* and *T. compactum* gave in every case slightly greater yields per plant than the average of the parents. On the other hand, F_1 crosses between durum or emmer varieties and varieties of common or club wheats were all significantly lower in yield than the parents. The low yields of these species

TABLE VII.—AVERAGE YIELD PER PLANT OF F_1 WHEAT CROSSES AND THEIR PARENTS

Name of one parent	No. of individuals	Yield, grams	Name of other parent	No. of individuals	Yield, grams	Average weight parents, grams	Cross	
							No. of individuals	Yield, grams
Marquis	15	1.9	Penny	36	2.4	2.2	18	2.7
Marquis	15	1.9	Bobs	59	3.0	2.5	65	3.3
Velvet Chaff	38	1.5	Penny	36	2.4	2.0	28	2.5
Velvet Chaff	38	1.5	Bobs	59	3.0	2.3	92	2.9
Penny	36	2.4	Bobs	59	3.0	2.7	23	2.8
Haynes Bluestem	47	2.4	Marquis	15	1.9	2.2	18	2.5
Marquis	15	1.9	Little Club	46	2.2	2.1	45	2.3
Velvet Chaff	38	1.5	Little Club	46	2.2	1.9	37	2.5
Average	30	1.9		45	2.5	2.2	41	2.7
Little Club	46	2.2	Emmer	48	1.1	1.7	9	0.3
Little Club	46	2.2	Mindum	49	2.1	2.2	1	1.0
Marquis	15	1.9	Mindum	49	2.1	2.0	13	0.3
Velvet Chaff	38	1.5	Mindum	49	2.1	1.8	8	1.1
Velvet Chaff	38	1.5	Emmer	48	1.1	1.3	23	0.5
Marquis	15	1.9	Emmer	48	1.1	1.5	18	0.6
Average	33	1.9		49	1.6	1.8	12	0.6

crosses are due in a large measure to sterility for there was an appreciably smaller setting of seeds in the crosses than in their parents.

Crosses between distinct species of self-fertilized plants have been carefully studied in the tobacco genus, *Nicotiana*. Results obtained may be summed up as follows (East and Hayes, 1912):

"(*a*) plants so different that they will not cross; (*b*) crosses that produce seed that contain no proper embryo; (*c*) crosses that produce seed with embryo, but which go no further than the resting stage of the seed; (*d*) crosses less vigorous than either parent; (*e*) crosses more vigorous than the average of the parents; and (*f*) crosses more vigorous than either parent."

Apparently in wide crosses the normal physiological processes are interfered with. The statement is frequently made that this is due to lack of compatibility between the parents. The specific physiological cause is not yet known.

EFFECTS OF SELF-FERTILIZATION IN NORMALLY CROSS-FERTILIZED PLANTS

This subject will be studied in relation to the specific outline for breeding some normally cross-fertilized plants, such as maize and rye. A few data will be presented in

order to illustrate the general results. The theoretical explanation is given, as an appreciation of these phenomena is essential in obtaining a correct plant breeding perspective.

The most extensive studies made have been those with maize. As this crop is almost entirely cross-pollinated under natural field conditions it is an admirable one to contrast with self-fertilized plants. Table VIII presents differences in yield and height obtained at the Connecticut Station with four self-fertilized strains of Leaming Dent. These strains were grown only in small plots, therefore differences are only indicative of the general results which may be expected. Crosses between individual plants within a strain that had been selfed six or seven years, were not appreciably more vigorous than the progeny of self-fertilized seed. These strains also differ in other characters, such as shape of ear, width of leaf, and color in various organs. One strain of Leaming Dent No. 1–12 was self-fertilized for about seven years. It produced well-developed tassels but few ears and was eventually lost.

TABLE VIII.—THE EFFECT OF INBREEDING ON THE YIELD AND HEIGHT OF MAIZE

Year grown	No. of generations selfed	The four strains							
		1-6-1-3, etc.		1-7-1-1, etc.		1-7-1-2, etc.		1-9-1-2, etc.	
		Yield, bu. per acre	Height, in.	Yield, bu. per acre	Height, in.	Yield, bu. per acre	Height, in.	Yield, bu. per acre	Height, in.
1916	0	74.7	117.3	74.7	117.3	74.7	117.3	74.7	117.3
1905	0	88.0		88.0		88.0		88.0	
1906	1	59.1		60.9		60.9		42.3	
				1907		1907			
1908	2	95.2		59.3		59.3		51.7	
				1908		1908			
1909	3	57.9		46.0		59.7		35.4	
1910	4	80.0		63.2		68.1		47.7	
1911	5	27.7	86.7	25.4	81.1	41.3	90.5	26.0	76.5
								1913	
1912	6							38.9	
								1914	
1913	7	41.8		39.4				45.4	85.0
								1915	
1914	8	78.8	96.0	47.2	83.5	58.5	88.0	21.6	
								1916	
1915	9	25.5		24.8				30.6	78.7
								1917	
1916	10	32.8	97.7	32.7	84.9	19.2	86.9	31.8	82.4
1917	11	46.2	103.7	42.3	78.6	37.6	83.8		

From these and other results (Jones, 1918) it is apparent that selfing in maize produces:

1. Strains which can not be perpetuated.
2. Strains which can be perpetuated only with difficulty.
3. Strains which exhibit normal development but vary in amount of growth attained.

EXPLANATION OF HYBRID VIGOR[1]

The studies of the early hybridizers, Koelreuter, Gärtner, Knight, and others, gave results which can be summed up in a single sentence as follows (East and Hayes, 1912):

"Crosses between varieties or between species often give hybrids with a greater vegetative vigor than is possessed by either parent."

Darwin made extended and careful studies of the effects of cross- and self-fertilization in plants. He conclusively proved that in general there is an advantage in cross-fertilization. While he noted some self-fertilized families he believed these would eventually perish. Lacking as he did a knowledge of Mendelian phenomena it was impossible for Darwin to develop as logical an explanation of these results as we now have. Darwin thought the results could best be explained by the nature of the sexual elements rather than in the act of crossing.

Several explanations of hybrid vigor have been advanced since the rediscovery of Mendel's law. In all cases heterozygosis has received a major place in the explanation. The results of these studies have been summed up as follows (East and Hayes, 1912):

"1. The decrease in vigor due to inbreeding naturally cross-fertilized species and the increase in vigor due to crossing naturally self-fertilized species are manifestations of one phenomenon. This phenomenon is heterozygosis. Crossing produces heterozygosis in all characters by which the parent plants differ. Inbreeding tends to produce homozygosis automatically.

"2. The phenomenon exists and is in fact widespread in the vegetable kingdom.

"3. Inbreeding is not injurious in itself, but weak types kept in

[1] A recent monograph by East and Jones (1919) presents in a clear and concise way the effects of inbreeding and cross-breeding in the light of modern theories of genetics. This publication has been used very freely in this section.

existence in a cross-fertilized species through heterozygosis may be isolated by its means. Weak types appear in self-fertilized species, but are eliminated because they must stand or fall by their own merits."

Biologists commonly believe that internal or external agencies do occasionally modify the germ plasm. It is also commonly accepted that somatic modifications do not impress themselves upon the germ plasm. From the facts of segregation as explained by the Mendelian law and the acceptance of the theory of factor stability, we may next consider what may be expected in self-pollinating a naturally cross-fertilized plant, such as corn, or what will result in later generations after making a cross in naturally self-fertilized plants.

Several slightly different formulæ have been advanced to show the theoretical expectation. The simplest formula for the percentage of homozygous types in any generation following a cross between different forms is $\left(\frac{2^n-1}{2^n}\right)^m$. In this formula n is the number of segregating generations which has elapsed since the cross was made and m is the number of separately inherited allelomorphic pairs of factors involved. In self-fertilized organisms this would not absolutely hold unless all the progeny of each genotype were equally productive numerically.

In artificially self-fertilizing naturally cross-pollinated plants, such as corn, it is theoretically possible to select a completely heterozygous individual in each generation for self-fertilization and thus obtain no reduction in heterozygosis. Jones (1919) has worked out theoretical curves for 1, 5, 10, and 15 allelomorphic pairs of factors for from one to 10 generations of self-fertilization following a cross.

Some facts regarding the effects of self-fertilization in generations following a cross are apparent from a consideration of this figure. When only a single allelomorphic pair is concerned, the first generation of selfing reduces the percentage of heterozygous individuals by half. When a number of factor pairs are concerned reduction of the percentage of heterozygous individuals is comparatively slow for the first few years of selfing. At the end of 10 years the percentage of heterozygotes is very low whether the initial cross was heterozygous for 15 allelomorphic pairs or for a single allelomorphic pair. From the above discussion it is apparent that after several years of self-fertilization following a

cross between different varieties a large percentage of the plants are homozygous and will breed true for their characters if self-fertilization is continued. The number of different biotypes which can be isolated from a cross depends upon the number of allelomorphic pairs of factors involved and their linkage relations.

Formerly the heterozygous condition was believed to carry with it an increased developmental stimulus. It was also believed that this stimulus was greater when the mate to an allelomorphic

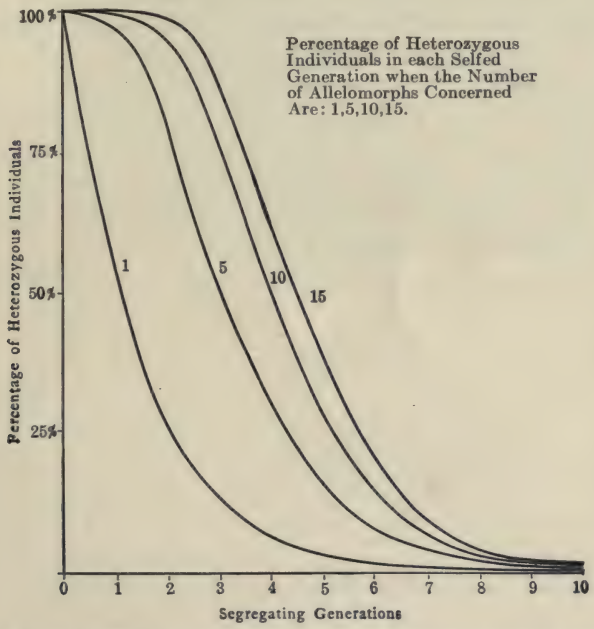


FIG. 12.—The percentage of heterozygous individuals and the percentage of heterozygous allelomorphic pairs in the whole population in each generation of self-fertilization. (*After Jones.*)

pair was lacking than when both were present. The physiological cause of this growth stimulus was not known although it was recognized that "the greater the degree of heterozygosis the greater is the vigor of the resulting plant" (East and Hayes, 1912). A considerable number of studies showed that the rapidity and amount of cell division was increased.

A Mendelian explanation of this growth stimulus which is so frequently found in crosses, has been advanced. Jones (1918) has explained the vigor of F_1 which has been called heterosis on the

basis of dominance and linkage. In comparing crosses with their parents it is quite common to find that the F_1 generation has a higher value for nearly every growth character than has the average of the parents. Modern geneticists recognize that each character is due to the interaction of many inherited factors. If each growth factor gives as great an effect when heterozygous as when homozygous or proves partially dominant when heterozygous, it would be easy to explain heterosis by the actual physiologicial growth development which is a part of the normal expression of a particular inherited factor. This explanation was formerly advanced to account for heterosis but was considered unreliable, as it was difficult to account for the almost universal decrease in vigor when such plants as maize were selfed. This can be explained by the facts of linkage, as it is possible to have a greater number of different growth factors present in a heterozygous than in a homozygous individual. The explanation has much in its favor.

CHAPTER IV

FIELD PLOT TECHNIC

In carrying out crop-breeding studies the number of varieties and strains has been greatly multiplied. Vilmorin's isolation principle, whereby the value of any selection is determined by the breeding nature of the progeny, has been universally adopted. The field is then the plant-breeder's laboratory and the question of correct field technic is of the utmost importance.

The difficulties, of making all conditions of similar nature for a large number of strains or varieties which must be tested, are very numerous. The method used must be such that the performance will be a correct indication of the comparative value of the strains being tested when grown under farming conditions. The purpose of the present chapter is to discuss field plot technic for such disturbing factors as soil heterogeneity and climatic conditions.

SOIL HETEROGENEITY

The field selected for the comparative trials should be representative of the soil and climatic conditions under which the crop will be grown. The land must then be cropped in such a manner that it is kept in a uniform state of good productivity. In order to do this, it is necessary to observe some one of the standard rotations. It is a good practice to have one or more bulk crops rotated with the breeding plots in order to keep the land uniform. If only one area of land is available there is then no choice and the investigator must see that this field is treated in the best possible way. If more than one field is available, it is possible to determine which is more nearly uniform by a correlation of contiguously grouped plots as outlined by Harris (1915).

Harris' Method of Estimating Soil Heterogeneity.—By Harris' method the coefficient of correlation is used as an index of soil uniformity . This statistical constant measures the degree of correlation between contiguous plots grouped in a certain way. If the variation in yield from plot to plot is simply due to random sampling, there will be no correspondence between contiguously grouped units. On the other hand, if the field is "patchy"

certain contiguous units tend to yield high while others show a tendency in the opposite direction. Under these conditions a high correlation coefficient results. If variability due to random sampling only is entering, the correspondence between some contiguous plots will be counterbalanced by the lack of correspondence between others, providing that the number of ultimate units is sufficiently large to permit an expression of the law of average. It is obvious that in the application of Harris' method the field must receive the same treatment (seed, cultivation, fertilizer, etc.). The division of the field into the desired units may be made at any time before the crop is harvested, but preferably before or soon after planting in order to minimize possible injury to the growing crop.

A simple illustration will make the calculation of the correlation coefficient clear, although a much larger number of units should be used in an actual study of the reliability of a field for plot work. Suppose a certain field is divided into 16 units and these units are in turn arranged in groups. Let p_1, p_2, p_3, etc., represent the ultimate units and C_{p_1}, C_{p_2}, etc., represent the groups. By assigning values for yield in bushels per acre to the ultimate units, one may make the calculation necessary to apply the formula. The value of any particular group is the sum of the ultimate units in it.

DIAGRAM ILLUSTRATING HARRIS' METHOD

(2) p_1 C	(2) p_2 p_1	(4) p_3 C	(6) p_4 p_2
(3) p_5	(3) p_6	(6) p_7	(4) p_8
(3) p_9 C	(3) p_{10} p_3	(5) p_{11} C	(5) p_{12} p_4
(5) p_{13}	(5) p_{14}	(4) p_{15}	(4) p_{16}

p = Average yield of all ultimate units = 4
n = Number of units in each group = 4
m = Number of groups = 4
$S(p^2)$ = Sum of squares of the yields assigned for ultimate units = 280
$S(C_p^2)$ = Sum of squares of the group yields = 1,080
σ_p = Standard deviation of assigned yield for the ultimate units = $\sqrt{1.5} = 1.2247$

$\sigma_p^2 = (1.2247)^2 = 1.4999$

The numbers enclosed in parentheses represent assumed values (bushels per acre).

Now according to the formula

$$r_{p_1p_2} = \frac{\{[S(C_p^2) - S(p^2)]/m[n(n-1)]\} - p^2}{\sigma_p^2}$$

Where $r_{p_1p_2}$ is the constant sought, S is indicative of summation, C_p the calculated values for the groups, p_1, p_2, etc., the assigned values for the ultimate units, m the number of groups, n the number of units in each group, p the average value of all the ultimate units and σ_p their standard deviation; we may, by substituting the given values, derive the coefficient of correlation.

$$r_{p_1p_2} = \frac{\{[1{,}080 - 280] \div 4[4(4-1)]\} - 4^2}{1.2247^2}$$

$$r_{p_1p_2} = \frac{16.6667 - 16}{1.4999} = \frac{0.6667}{1.4999} = 0.444 \pm 0.135^1$$

The magnitude of the coefficient obtained may be influenced by the size of the ultimate and group units, the nature of the character measured, and the variety or strain grown.

The above-outlined method is especially useful where it is desirable to determine the relative heterogeneity of several fields. The application of this test for uniformity to a field that is being used for experimental work would, in many cases, prevent the use of the field for breeding operations for at least a year.

Estimating Soil Heterogeneity by Means of Checks.—Check plots are often used in determining the comparative soil variability of fields that are being used for plot studies. This is done by the calculation of statistical constants. When used for this purpose checks should be systematically placed over the entire experimental area. The number should be large in order that an approach to a normal frequency distribution may be obtained, and systematic distribution should be followed in order to insure a representative random sample. Comparison of soils should be made in the same year and by the use of the same strain as the check. In general, the greater the degree of soil heterogeneity the greater will be the calculated standard deviation, coefficient of variability, and probable error.

Use of Checks in Correcting Yields.—Aside from the use to indicate soil variation, checks plots have often been used to make direct corrections for yield. Table IX, taken from Wood and Stratton (1910), illustrates a simple use of checks

[1] P. E. coefficient of correlation $= \frac{\pm 0.6745\ (1 - r^2)}{\sqrt{n}} = \frac{\pm 0.6745\ (1 - 0.444^2)}{\sqrt{16}} = \pm 0.135.$

for the purpose of correcting yields where there is a tendency to vary in one direction across a field.

TABLE IX.—DIRECT CORRECTION FOR YIELD WHERE VARIATION IS IN ONE DIRECTION ACROSS A FIELD

	Yield of $\frac{1}{28}$-acre plots, lb.	Correction, lb.	Corrected yields, lb.
	2,537	−12 × 25	2,237
	2,515	−11 × 25	2,240
Mean 2,640	2,866	−10 × 25	2,616
	2,648	− 9 × 25	2,423
	2,636	− 8 × 25	2,4 6
	2,581	− 7 × 25	2,406
	2,814	− 6 × 25	2,664
	2,944	− 5 × 25	2,819
Difference	2,748	− 4 × 25	2,648
between means	2,593	− 3 × 25	2,518
500 lb.	2,567	− 2 × 25	2,517
	2,357	− 1 × 25	2,332
	2,415	0 × 25	2,415
Correction	2,424	+ 1 × 25	2,449
from plot to	2,423	+ 2 × 25	2,473
plot $\frac{500}{20}$	2,399	+ 3 × 25	2,474
= 25 lb.	2,272	+ 4 × 25	2,372
	2,374	+ 5 × 25	2,499
	2,123	+ 6 × 25	2,273
	2,273	+ 7 × 25	2,448
	2,117	+ 8 × 25	2,317
	2,001	+ 9 × 25	2,226
Mean 2,140	2,115	+10 × 25	2,365
	2,246	+11 × 25	2,521
	2,222	+12 × 25	2,522
	P.E. ± 7 per cent.		P.E. ± 4 per cent.

In the second column of Table IX the actual yields are given of 25 contiguous $\frac{1}{28}$-acre plots across a field. The figures show a more or less gradual decrease, reading from top to bottom.

There is a difference of 500 lb. between the average yield of the first five plots and the average yield of the last five plots, or an average difference from plot to plot of 25 lb. This correction is applied by adding to those on one side and subtracting from those on the other side of the centrally located plot. The amount added or substracted depends on the distance from the center,

i.e., a progressive difference of 25 lb. for each plot in either direction from the central one. The corrected yields are found in the last column of the table. Note that the probable error is 3 per cent. less in the corrected than in the uncorrected yields.

The method outlined above may be used only where there are a comparatively large number of similarly treated plots and where the increase or decrease in yield across a field is fairly consistent. If check plots are grown every third to fifth plot as they frequently are, a direct correction for yield is sometimes made as follows:

DIAGRAM ILLUSTRATING DISTRIBUTION OF CHECKS

C	1	2	3	C_1	4	5	6	C_2

Suppose every fourth plot is a check. The productivity of each intervening plot is estimated on the basis of the yields of the two nearest checks. For instance, the true productivity for plot one equals $\frac{3}{4}C + \frac{1}{4}C_1$; for plot two equals $\frac{1}{2}C + \frac{1}{2}C_1$; for plot three equals $\frac{1}{4}C + \frac{3}{4}C_1$; etc. For example, by this method the yielding value of plot six could be obtained. The corrected yield could then be obtained by the following proportion: Average yield of all check plots: yielding value of plot six = the actual yield obtained from plot six: X. In a similar way corrected yields could then be obtained for all plots in the test.

Use of Checks as a Probable Error of the Experiment.—Other methods of using the checks as direct corrections for yield have been employed, but the tendency in present-day field investigations is away from the use of checks for this purpose (especially where yield is being studied). They are, however, very valuable indices of soil variation, thus giving an approximate measurement of reliability for the particular experiment. To illustrate the use of checks in this way, suppose in a certain experiment there were 50 systematically distributed checks grown and that the computed probable error of a single check plot (standard deviation $\times$ 0.6745) was 4 bu. Suppose each variety or strain being investigated for yield is replicated three times, making four plots in all. The probable error of the average yield of these four plots would be equal to the probable error of a single check, 4 bu. divided by the square root of the number of plots, or 4. This gives 2 bu. as the probable error of the average yield of

four plots. Using this figure as a basis, a direct comparison may be made between the average yield of any two strains in terms of their probable errors. To carry our hypothetical problem still further, suppose the average yield of four plots of strain *A* was 20 bu. while that of strain *B* was 26 bu. As the probable error of each average is 2 bu., and the probable error of a difference is equal to the square root of the sum of the squares of the probable errors of the two quantities, we would have

$$\begin{array}{r} 26 \pm 2 \\ 20 + 2 \\ \hline 6 \pm \sqrt{4+4} \text{ or } 6 \pm 2.8 \end{array}$$

The difference is only a little more than two times its probable

TABLE X.—PROBABILITY OF OCCURRENCE OF STATISTICAL DEVIATIONS OF DIFFERENT MAGNITUDES RELATIVE TO THE PROBABLE ERROR

Deviation divided by P.E.	Probable occurrence of a deviation as great as or greater than designated one in 100 trials	Odds against the occurrence of a deviation as great as or greater than the designated one	Deviation divided by P.E.	Probable occurrence of a deviation as great as or greater than designated one in 100 trials	Odds against the occurrence of a deviation as great as or greater than the designated one
1.0	50.00	1.00 to 1	3.5	1.82	53.95 to 1
1.1	45.81	1.18 to 1	3.6	1.52	64.79 to 1
1.2	41.83	1.39 to 1	3.7	1.26	78.37 to 1
1.3	38.06	1.63 to 1	3.8	1.04	95.15 to 1
1.4	34.50	1.90 to 1	3.9	0.853	116.23 to 1
1.5	31.17	2.21 to 1	4.0	0.698	142.26 to 1
1.6	28.05	2.57 to 1	4.1	0.569	174.75 to 1
1.7	25.15	2.98 to 1	4.2	0.461	215.92 to 1
1.8	22.47	3.45 to 1	4.3	0.373	267.10 to 1
1.9	20.00	4.00 to 1	4.4	0.300	332.33 to 1
2.0	17.73	4.64 to 1	4.5	0.240	415.67 to 1
2.1	15.67	5.38 to 1	4.6	0.192	519.83 to 1
2.2	13.78	6.26 to 1	4.7	0.152	656.89 to 1
2.3	12.08	7.28 to 1	4.8	0.121	825.45 to 1
2.4	10.55	8.48 to 1	4.9	0.095	1,051.63 to 1
2.5	9.18	9.89 to 1	5.0	0.074	1,350.35 to 1
2.6	7.95	11.58 to 1	6.0	0.0052	19,230.00 to 1
2.7	6.86	13.58 to 1	7.0	0.00023	434,782.00 to 1
2.8	5.90	15.95 to 1	8.0	0.000000068	1,470,588,234.00 to 1
2.9	5.05	18.80 to 1			
3.0	4.30	22.26 to 1			
3.1	3.65	26.40 to 1			
3.2	3.09	31.36 to 1			
3.3	2.60	37.46 to 1			
3.4	2.18	44.87 to 1			

error and, therefore, under the assumed conditions of the experiment, of little significance, as is indicated by Table X taken from Pearl and Miner (1914).

Use of Probable Error in Eliminating Strains.—The probable error obtained by means of the checks may also aid in selecting an elimination value below which varieties or strains may be discarded without danger of throwing away a valuable one. This figure is necessarily more or less arbitrary and will depend upon the desired degree of accuracy. The magnitude of the figure which is multiplied by the probable error will also depend somewhat upon the desired amount of elimination. The method used at the Minnesota Station is to subtract the product of three times the probable error for the method of test multiplied by $\sqrt{2}$ from the highest or one of the higher yielding strains. The difference gives a figure below which it is considered safe to discard without danger of eliminating a high yielding strain. If the yield of a strain falls below the elimination figure for two or three years, it is discarded from further trials.

The Pairing Method of Securing a Probable Error.—Under certain conditions it is impracticable to devote so large a share of the experimental field to check plots. Wood and Stratton (1911) have suggested a means of securing a reliable probable error without the aid of checks. Briefly, their method consists of systematically pairing similarly treated plots and finding their mean yields. The deviation of this mean from the yield of the original plots is expressed in percentage of the mean. The following illustrates the procedure:

Plot arrangement	A′	B′	C′	etc.	A″	B″	C″	etc.	A‴	B‴	C‴	etc.
Yield per acre	20	22	24	etc.	21	23	25	etc.	24	22	23	etc.

Now if all A plots are similarly treated, A' would be paired with A'' and A'' with A''', etc.

In this method the probable error is expressed in percentage of the mean. If the number of pairs is sufficiently great the deviations + and − will yield a normal frequency curve. As in the method of determining the probable error by means of checks, it is desirable to have a large enough number of variants to secure at least an approach to the normal frequency distribution.

TABLE XI.—The Pairing Method

Plot	Yield	Mean	Deviation	Deviation in percentage of mean	Deviation in percentage of mean squared
A'	20	20.5	0.5	2.4	5.76
A''	21				
A''	21	22.5	1.5	6.7	44.89
A'''	24				
etc.					
Total	86		2.0	9.1	50.65
Average	21.5		1.0	4.6	25.33

After the deviations have been converted into percentages of the mean, their sum is divided by n where n is the number of pairs. By multiplying the average yield of all plots by this percentage, a probable error for yield of a single plot may be obtained.

Wood and Stratton (1910) present the following probable errors obtained by the pairing method, based on a large number of replicated plots including the different crops—wheat, barley, oats, mangels, rutabagas, potatoes, and seed grasses.

400 pairs of plots, different sizes..... P.E. 4.2 per cent.
45 pairs of plots, each ½ acre..... P.E. 3.5 per cent.
52 pairs of plots, each ¼ acre..... P.E. 3.5 per cent.
29 pairs of plots, each 1/20 acre..... P.E. 3.9 per cent.
200 pairs of plots, each 1/40 acre..... P.E. 4.6 per cent.
75 pairs of plots, each 1/80 acre..... P.E. 3.1 per cent.

In applying the method of Wood and Stratton at the Minnesota Experiment Station it was found that a slight modification usually gave probable errors which more nearly approached those obtained by the use of check plots. The modification consisted of squaring the deviations before dividing by n and extracting the square root of the quotient. This calculation is given in the last column of the preceding table.

Replication and Its Value.—It has been found that systematic repetition of the plots reduces the probable error and hence increases the significance of the results. The number of replications necessary in order to make reliable comparisons is somewhat dependent on the kind of crop but to a greater extent on soil heterogeneity. If it were desired to establish a significant difference of as little as 2 bu. between varieties, more replications would be needed than if a significant difference of 4 bu. was accepted as satisfactory. Several investigations have been re-

ported which for the particular condition of the experiment show the number of replications desirable.

Mercer and Hall (1911), of England, recommend the use of five systematically distributed plots of $\frac{1}{40}$ acre each. Montgomery (1913), in his work at Nebraska, found that 16 ft. rows gave best results when repeated from 10 to 20 times. At the Cornell Experiment Station, when a careful yield test is desired each strain is grown in 10 distributed rod rows.

In the plant-breeding nursery of the Minnesota Experiment Station the practice is followed of growing each strain in a plot consisting of three rod rows. The plots are replicated three times, making four plots in all. The central rows only are harvested. Table XII taken from Hayes and Arny (1917) shows the effect of replication based on the yield of the central rows of the wheat checks grown in 1916.

TABLE XII.—VALUE OF REPLICATION BASED ON 72 CENTRAL ROWS OF THREE-ROW PLOTS OF TURKEY WINTER WHEAT (MINN. 529) GROWN IN THE PLANT BREEDING NURSERY

Number of replications	Number of variables	Mean yield per acre	Standard deviation
None	72	27.5±0.4	4.65±0.26
One (average of 2 plots)	36	27.6±0.3	2.98±0.24
Two (average of 3 plots)	24	27.4±0.3	2.51±0.24
Three (average of 4 plots)	18	27.6±0.2	1.49±0.17
Five (average of 6 plots)	12	27.3±0.4	2.01±0.28
Eleven (average of 12 plots)	6	27.3±0.3	1.21±0.24

While the standard deviations do not decrease according to theoretical expectation they do show a marked decrease up to and including three replications. The table shows that variability is rapidly diminished by replication up to a certain number. In general, beyond this point it is questionable whether the relatively small gain in accuracy warrants the additional work. The results obtained at the Minnesota Station indicate that plots of three rod rows each or $\frac{1}{40}$-acre plots sown with the ordinary grain drill, give about as accurate a comparison for yield when replicated three times as when replicated eight times.

The manner of making replications is another factor to be considered. If the experimental plots are all planted in a single

series then replication becomes a matter of systematic repetition as is shown by the following diagram in which each different letter represents a distinct strain.

A METHOD OF REPLICATION

A	B	C	D	E	F	G	H	A	B	C	D	E	F	G	H	A	B	C	D	E	F	G	H	A	B	C	D	E	F	G	H

As a rule the experimental plots cannot all be placed in the same series. It is often necessary to make alterations from a mere systematic repetition in order to secure a representative distribution of the strains. The two following diagrams illustrate a correct and an incorrect manner of replication:

CORRECT MANNER OF REPLICATION

A	J	G	D
B	K	H	E
C	L	I	F
D	A	J	G
E	B	K	H
F	C	L	I
G	D	A	J
H	E	B	K
I	F	C	L
J	G	D	A
K	H	E	B
L	I	F	C

INCORRECT MANNER OF REPLICATION

A	A	A	A
B	B	B	B
C	C	C	C
D	D	D	D
E	E	E	E
F	F	F	F
G	G	G	G
H	H	H	H
I	I	I	I
J	J	J	J
K	K	K	K
L	L	L	L

Size of Plot.—The number of replications required to secure a given degree of accuracy is somewhat dependent on the area of the plot. Mercer and Hall (1911) found that variability is diminished with increased size of plot up to $\frac{1}{40}$ acre. Plots of larger area do not show the same relative reduction in variability. Fig. 13 presents graphically their results with wheat.

Montgomery (1913) also finds that increased size of plot, up to a certain limit, rapidly decreases variability. In plant-breeding work where very numerous strains are compared, the

size of plot is necessarily limited by available space and sometimes by amount of seed. Some form of row planting is usually followed. These rows are planted, cultivated, and harvested by hand and frequently show as low probable errors as those obtained from $\frac{1}{40}$-acre field plots.

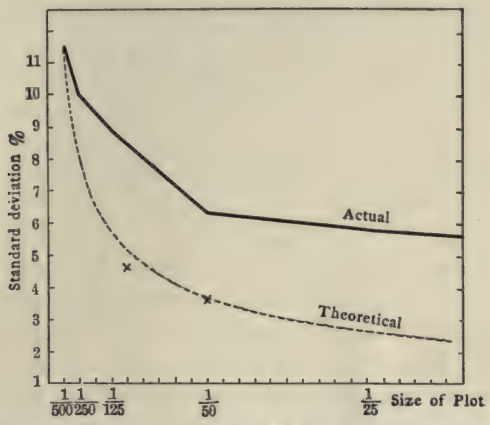


FIG. 13.—Actual and theoretical reduction in standard deviation due to increase in size of plot.

Shape of Plot and Border Effect.—Often plants growing along the side or end of the plot are more thrifty and vigorous than those growing in the interior. When plots consist of single rows, the plants at the extremities near the alleys or pathways appear superior to those growing farther in.

Mercer and Hall (1911) cut up a bulk field into plots of equal area but different in shape (approximately 20 by 12 yd. and 50 by 5 yd.) and therefore without border effect. No significant difference in comparative variability was found between the two shapes. Barber (1914) found that where cultivated pathways surrounded plots, the plants along the margins were more productive than those within the plot.

Table XIII presents data collected by Arny and Hayes (1918). The plots were seeded with a grain drill, the drill rows being 6 in. apart. Eighteen-inch alleys separated the plots, and there was a roadway along each end. In length the plots were trimmed to 132 feet. In breadth they were 17 drill rows, each 6 inches apart. Each of the two outside border rows was harvested separately and the yield compared with the yields obtained from the

central rows. The plants on each end of the plots to a depth of at least a foot were cut and discarded.

TABLE XIII.—COMPARISON OF AVERAGE YIELD OF OATS, WHEAT AND BARLEY HARVESTED FROM BORDER ROWS AND CENTRAL ROWS PLOTS 132 BY 8.5 FT.

Source	Oats		Wheat		Barley	
	No. of plots	Yld. per acre, bu.	No. of plots	Yld. per acre, bu.	No. of plots	Yld. per acre, bu.
Outside border rows	44	132.0	20	55.0	16	97.7
Inside border rows	44	88.0	20	41.0	16	64.5
Central 13 rows	44	71.4	20	27.5	16	42.9

It is clear from Table XIII that border effect may profoundly influence yield. Long, narrow plots have a larger proportion of their area in border than those which more nearly approach a square. This would seem to indicate that square plots should be given preference over oblong ones unless the borders are discarded. As a matter of fact, most workers use long, narrow plots because of the greater ease with which they may be seeded and harvested with machinery. Furthermore, border effect may be entirely removed by discarding the borders and ends of the plot.

The removal of borders becomes still more desirable when the fact is considered that different strains and varieties may react unequally to borders or ends. Evidence has been accumulated which shows that some strains utilize the border to a greater degree than others. Obviously those strains which gain least from the alley space will not be given a fair trial unless border rows are discarded from all the plots in the experiment. Conversely, those which have the greater ability to use the border may be given a higher rating than they deserve unless the borders are removed.

It would seem from the evidence presented that it is highly desirable to discard ends and borders to a depth of at least a foot in the case of rectangular plots and a foot at each end in the case of rod rows growing side by side.

Competition as a Factor in Plot Variability.—Competition between nearby strains, particularly under certain experimental conditions, may seriously influence results. A tall variety may

hamper a shorter one, or a vigorous grower may inhibit one that grows more slowly. The existence of competition between adjacent strains or varieties has been definitely proved at several experiment stations. The work of Kiesselbach (1918) at the Nebraska Station is particularly illuminating on this point. Kiesselbach compared competition between adjacent single row plots and adjacent plots each consisting of from three to five rows. The yield of border rows was in some instances included in the yield of the blocks. His results are summarized in Table. XIV.

TABLE XIV.—SUMMARY OF RELATIVE GRAIN YIELDS OF VARIETIES TESTED IN SINGLE-ROW PLOTS AND ALSO IN BLOCKS CONTAINING SEVERAL ROWS

Varieties compared in alternating rows and in alternating blocks	Year of test	Ratio of variety No. 1 to variety No. 2		
		Alternating rows	Alternating blocks	Competing in same hill
Turkey Red (1) and Big Frame (2) winter wheat	1913	100:107	100:97	
Turkey Red (1) and Big Frame (2) winter wheat	1914	100:85	100:97	
Turkey Red (1) and Nebraska No. 28 (2) winter wheat	1913	100:107	100:107	
Turkey Red (1) and Nebraska No. 28 (2) winter wheat	1914	100:63	100:85	
Kherson (1) and Burt (2) oats	1913	100:130	100:112	
Kherson (1) and Burt (2) oats	1914	100:139	100:101	
Kherson (1) and Swedish Select (2) oats	1913	100:82	100:77	
Kherson (1) and Swedish Select (2) oats	1914	100:89	100:93	
Hogue's (1) and Pride of the North (2) corn	1912	100:66	100:85	100:47
Hogue's (1) and Pride of the North (2) corn	1914	100:38	100:53	100:26
Hogue's (1) and University No. 3 (2) corn	1914	100:90	100:98	100:99
Crossbred Hogue's (1) and inbred Hogue's (2) corn	1916	100:31	100:37	100:21

A comparison of the columns in Table XIV headed alternating rows and alternating blocks shows strikingly the effects of competition. In almost every case the varieties grown in alter-

nating rows show a greater difference than the same varieties grown in alternating blocks. Perhaps the extreme effect of competition is shown by different varieties of corn grown in the same hill.

In the plots consisting of three rows each, grown at the Minnesota Experiment Station in 1916, a study of competition was made. When varieties of different heights were grown in adjacent plots a considerable effect was obtained in the yields of border rows in the barley and winter wheat nurseries. The effect of competition has been observed at other experiment stations and various ways of overcoming its possible vitiating influence have been suggested.

One of the easiest and most effective means of eliminating this source of error is by the use of sufficiently wide borders which are discarded at harvest. In the case of plots, consisting of a single row, it is possible to make the planting plan in such a way as to minimize effects of competition. The rows should be laid out north and south and the varieties and strains most nearly alike in habits of growth should appear side by side. At best this method can do no more than decrease the error due to competition, while the elimination of effective borders overcomes competition. The use of borders necessitates a larger experimental area and is somewhat more expensive for a given number of trials.

CLIMATIC VARIATIONS

One other disturbing factor to be considered in conducting plot tests is variation induced by weather conditions. Its presence is so obvious to any one who has worked with growing crops that further comment is hardly necessary. In a year of deficient rainfall the varieties best qualified to subsist under a minimum water supply will yield most. Some seasons are better for the growth of early maturing varieties than for late ones. An epidemic of a plant disease like rust may be fostered or hampered by weather conditions. The question arises, how may errors due to this source be overcome? Conducting an experiment over a period of years is the only effective means at the disposal of the investigator. The strain which fluctuates the least from year to year and also gives a high average performance is most valuable for the farmer.

SUMMARY OF FIELD PLOT TECHNIC

Following is a brief summary of the more important factors which assist in obtaining reliable plot results.

1. Soil heterogeneity exists in varying degrees, hence uniform plots should be selected for the field experiments. To aid in determining the comparative uniformity of different fields, Harris' method or the check plot method may be used.

2. If the field varies uniformly from one side to the other, check plots may be used to correct yields. In general, the use of checks to correct yields is undesirable.

3. The yield of check plots may be used to determine the probable error of the method of work. They should be placed systematically throughout the experimental plots and the number should be sufficiently large to approach a normal frequency distribution.

4. Probable errors may be used to determine whether the obtained differences between strains are significant and thus aid in eliminating the significantly lower yielders.

5. The probable error of an experiment may be determined by the pairing method suggested by Wood and Stratton. It is comparable to the one based on the checks and may be used in the same way.

6. The probable error of an experiment may be reduced most effectively by plot replication. Replication up to a certain number rapidly reduces the probable error, beyond that number additional replications do not proportionately decrease it. The number of replications will depend considerably on the character of the soil and somewhat on the size of the plots. On fairly uniform land three replications have been found satisfactory for general breeding studies.

7. Oblong plots sown with an ordinary grain drill give reliable results when their area is approximately $\frac{1}{40}$ acre each.

8. Plants growing on the border of a plot adjacent to an alley or roadway are usually superior to those growing within the plot, hence, if it is desired to secure yields comparable with those which would be secured under field conditions, the border plants must be discarded. The border should be removed to a depth of at least a foot. Different varieties and strains may have unequal ability to utilize the free space along the pathways between plots and consequently a second reason arises for discarding the border.

9. Competition exists between nearby varieties and strains.

The grouping of varieties and strains so that those of similar habits of growth appear side by side removes to a considerable degree the evil effects of competition. The most effective means of overcoming competition is by the use of sufficiently wide borders which are discarded at harvest.

10. Results of field tests vary from year to year because of changing weather conditions, and for this reason it is necessary to extend a test over a period of several years. For varietal trials a minimum of three years is recommended.

CHAPTER V

CONTROLLING POLLINATION

Methods of controlling pollination have received considerable attention. Protecting self-fertilized plants from occasional natural crosses would seem to be a necessity in careful studies of heredity. The lack of technic of crossing may be a cause of failure to improve a particular crop. This entire field is one in which actual practice is needed before the worker can hope to accomplish best results. A few general principles will be given.

Selfing Plants Artificially.—Certain methods have already been worked out for particular crops. As an example, in the tobacco crop artificially self-fertilized seed may easily and cheaply be produced. The practical grower can well afford to save his seed by this practice. Before any of the blossoms have opened, the terminal inflorescence should be covered with a manila paper bag. The 12-lb. size has been found satisfactory for this purpose. If a few flowers have already been pollinated these may be removed before bagging. After a week or 10 days has elapsed, the bag should be taken off and all flowers except from 50 to 60 removed and the dead corollas shaken off. After sufficient flowers have been fertilized the bag may be removed, as the seed will mature somewhat more rapidly than when enclosed.

Self-pollination of the tomato may be accomplished in very much the same manner as with tobacco. Small-sized bags are needed. In this case it is necessary to jar the flowering branches upon which the bags are placed as the tomato does not set seed freely unless some such practice is followed.

Artificial self-pollination in corn is very easy. The ear and tassel may each be covered with a 12-lb. manila paper bag. It is necessary to cover the ear before any of the silks show. Foreign pollen accidentally enclosed with the tassel will not function after a period of more than two days. Approximately two to five days after the ear has been bagged the silks will have grown out and will be ready for pollination. The most favorable time for pollination is when the silks are 2 to 3 in. long, although the silks are receptive when much longer.

Two men may well work together in pollination. One unties the ear bag and the other shakes the dead anthers from the tassel bag and pours the pollen over the silk. Care is needed in performing this operation to prevent cross- or uncontrolled pollination. In producing biotypes by self-fertilization the occasional cross may easily be rogued out as the crossed plant will plainly be seen the following year because of its vigor and other characters. Some workers prefer transparent paper bags which allow the development of the silks to be noted without removing the bag from the ear, and thus save unnecessary work.

Hard showers or long continued rains seriously interfere with the artificial pollination of corn, as the tassel bag becomes wet and makes the handling of the pollen difficult. A desirable method is to remove the tassel bags after each rain and put on new ones. As a number of days elapse from the time the first pollen of the tassel matures until all is mature, the method of replacing tassel bags gives good results.

Self-pollination of squash has been carried out at the Minnesota Station. A little practice helps in determining when a flower is about ready to open. The petals of both staminate and pistillate flowers are prevented from opening by placing a small rubber band around each one. On removing the band the following day the flower quickly opens if it is ready for pollination. The petals are then removed from the staminate flower and the anthers rubbed over the pistil. The artificially pollinated flower is protected from cross-pollination by placing a rubber band around the petals. After a few days the petals of the crossed flower abciss and at this time the stigma has turned brown and is no longer receptive. This method was worked out by John Bushnell, a graduate student in horticultural plant breeding. From a total of 600 pollinations made under field conditions in the summer of 1919, approximately 150 set fruit.

Technic of Crossing.—A thorough knowledge of flower structure of the species or variety to be worked with is essential before crossing is undertaken. It is important to know which flowers are the most vigorous and which set fruit the most freely. Many varieties of wheat, for example, produce several seeds per spikelet. The outer florets of the spikelets in the central part of the rachis are more vigorous and usually produce larger seed. In some *Solanaceæ* (for example, the petunia) the later flowers form larger, healthier seed than those which first open (East,

1910*c*). After becoming familiar with the flower structure it is important to determine at what time of day the pollen is most easily collected and for what length of time the stigma is receptive. Environmental conditions modify the expression of these and other characters. However, some general rules for different groups of crops may be given.

Certain tools are essential for the work of pollination. For general work these are a small pair of thin, pointed scissors; a pair of forceps with thin, pointed blades which meet exactly and which are not too stiff; one or two dissecting needles; a hand lens; a pencil; and small string tags for recording purposes. Other special apparatus is necessary for difficult crosses.

Crossing of Small Grains.—The technic of small grain crossing is comparatively simple. Some practice, however, is necessary in order to gain proficiency and to obtain a fair percentage of seeds set. In some of the earlier directions it was stated (Hays, 1901) that it was necessary to make crosses of wheat at about 4 o'clock in the morning. Leighty and Hutcheson (1919) have determined the period in which blooming takes place at University Farm, St. Paul, Minn., and at Arlington Farm, Rosslyn, Va. The spikes were examined at 7 a.m., 12 n., and 5 or 6 p.m. A flower was considered as having bloomed when the glumes had opened appreciably. The period from 5 or 6 p.m., to 7 or 8 a.m. was referred to as night. Of 2,977 wheat flowers on 69 spikes, 1,492 bloomed at night and 1,485 bloomed during the day. About half of those which bloomed during the day bloomed before noon. These figures are given to correct the erroneous idea that it is always necessary to pollinate wheat early in the morning. Environmental conditions may be an important factor, for Salmon (1914), working in South Dakota, stated that blooming was practically completed before 7 o'clock in the morning.

Leighty and Hutcheson (1919) show that in wheat it is unsafe to leave the spikes uncovered after emasculation. Seeds were formed by 507 of 1,240 emasculated, unprotected flowers at University Farm, Minn. and 1,103 seeds were formed in 1,324 flowers similarly handled at Arlington Farm, Va. while less than 1 per cent. of flowers emasculated and covered with paper bags set seed. Frear (1915), working with Turkey winter wheat, obtained 80 per cent. seeds set on emasculated, uncovered spikes and less than 1 per cent. on emasculated covered spikes.

A common practice used at Minnesota University Farm is to emasculate a number of spikes one day and make the crosses from one to four days later at about the time when the flowers open.

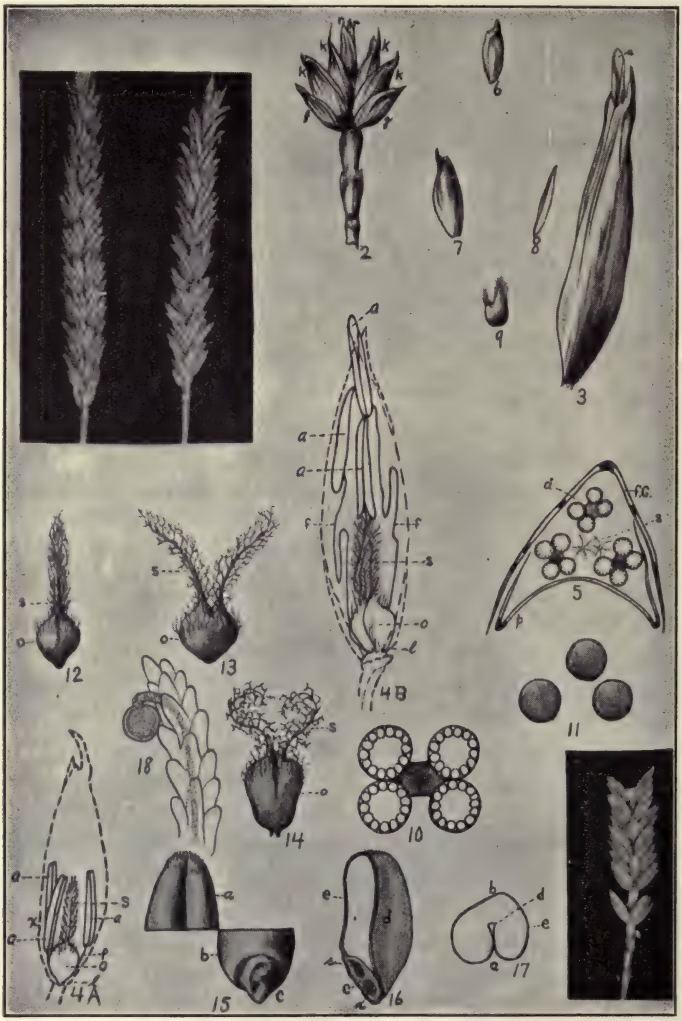


FIG. 14.—Details of wheat inflorescence.

Upper left, normal spikes; lower right, emasculated spike; 2, spikelet natural size; *f* and *g*, flowerless glumes; *k* and *r*, florets; 3, a single flower closed just after flowering, 3*n*; 4*A*, longitudinal diagram before flowering, x 2.5*n*, *a* = anthers, *o* = ovary, *s* = stigma, *f* = filament; 4*B* = diagram after flowering; 5 = transverse floral diagram, 6*n*, *fg* = lemma, *p* = palea, *a* = anthers, *s* = stigma; 6, flowerless glume, 7, lemma, 8, palea, slightly reduced; 9, lodicule, 4*n*; 10, cross-section anther, 26*n*; 11, pollen grains; 12, ovary and stigma just prior to flowering; 13, at flowering; and 14, shortly after; 15, 16, 17, the mature seed. (*After Babcock and Clausen*, 1918, *after Hays and Boss.*)

All but the outer florets of eight of the central spikelets are removed. The upper and lower spikelets are cut off with shears and the central floret of each remaining spikelet is removed by grasping it near the top with the forceps and giving a downward pull. The forceps are then carefully pushed between the palea and lemma and the flower opened. The three stamens are removed in one operation, if possible. Care is taken not to pinch the anthers too tightly and break them open. Spikes are used in which the anthers are just beginning to turn yellow. Anthers from the variety to be used as the pollen parent are removed from the florets. Experience has shown that it is best to use only anthers which are ready to dehisce and which open after being held in the hand or soon after being placed in a watch glass in the sun. A single ripe anther is introduced into each floret.

Where greenhouse facilities are available, crosses may advantageously be made in the winter or early spring months. This method is used extensively by the Plant Breeding department of Cornell University. When all conditions are favorable, between 50 and 100 per cent. of crossed seeds may be obtained.

Barley and oats are handled in nearly the same manner as wheat. With barley it is often necessary to emasculate before the spikes have entirely protruded from the leaf sheath. The work is somewhat more difficult, as the flowering parts are much more tender than in wheat. For this reason forceps and shears with very fine points and thin blades are needed. Apparently under certain environmental conditions (Arlington Farm, Va., Norton, 1902) and likewise at University Farm, Minn., oat flowers nearly all bloom in the late afternoon. Artificial pollination under these conditions is more easily performed in the afternoon from one o'clock until mature pollen is no longer easily collected.

Among the difficulties of artificial crossing in the field are unfavorable weather conditions. Too much rain or long-continued rains prevent work. Jellneck (1918) compared two methods of crossing wheats: (1) emasculation and pollination by placing a ripe anther in the floret; (2) emasculating spikes as usual and tying these with spikes of similar maturity belonging to the pollen parent and covering with a paper bag. In 1916 method (2) gave twice as great setting of seed as method (1). In 1917 conditions were very unfavorable and no seed was produced by

method (1), while method (2) gave seeds in 24 out of 47 spikes. On these 24 spikes 50 per cent. of florets produced seeds.

Crossing Large-flowered Legumes.—Oliver (1910) of the United States Department of Agriculture, has made excellent contributions to the technic of crossing. He emphasizes the fact that in a cross between self-fertilized varieties, only a few seeds are needed in F_1. The large-flowered legumes, such as Lathyrus, Phaseolus, Pisum, Stizolobium, and Vigna, should be emasculated in the bud stage. The following account of crossing Vigna, the cowpea, is taken from Oliver.

"In the evening it is found that the buds which will expand the next morning are quite large and easily manipulated in emasculating (*A*).

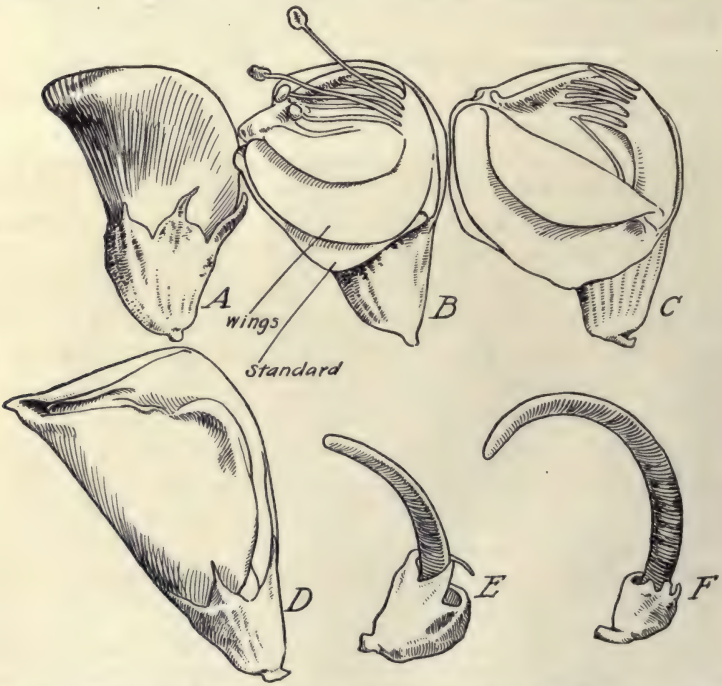


FIG. 15.—Flowers and young pods of the cowpea (twice natural size). (*Copied from photograph by Oliver.*)

A, Flower bud showing condition on the evening of the day previous to opening of flower; *B*, flower in the bud stage showing how the floral envelope is opened to gain access to stamens for emasculation; *C*, flower with stamens removed showing the large stigma to the left; *D*, emasculated flower the next morning after pollination; *E*, the young pod the second morning after pollination; *F*, the same pod forty-eight hours after the pollination of the flower. (*After Oliver.*)

Hold the bud between the thumb and forefinger with the keeled side uppermost (*B*); then run a needle along the ridge where the two edges of the standard unite. Bring down one side of the standard, securing it in position with the thumb; then do the same with one of the wings, which will leave the keel exposed. This must be slit on the exposed side about ⅛ in. below the bend in the keel and continuing along until about 1/16 in. from the stigma, which can be seen through the tissue of the keel. Bring down the section of the keel and secure it under the end of the thumb. This will expose the immature stamens, 10 in number. With a fine-pointed pair of forceps seize the filaments of the stamens and pull them out, counting them as they are removed to make certain that none are left (*C*). Allow the disturbed parts of keel, wings, and standard to assume their original positions as far as possible. Next detach a leaflet from the plant, fold it once, place it over the emasculated flower bud, and secure it in position with a pin or toothpick."

This prevents drying out. Flowers so treated and pollinated the next morning gave a large percentage of successful crosses.

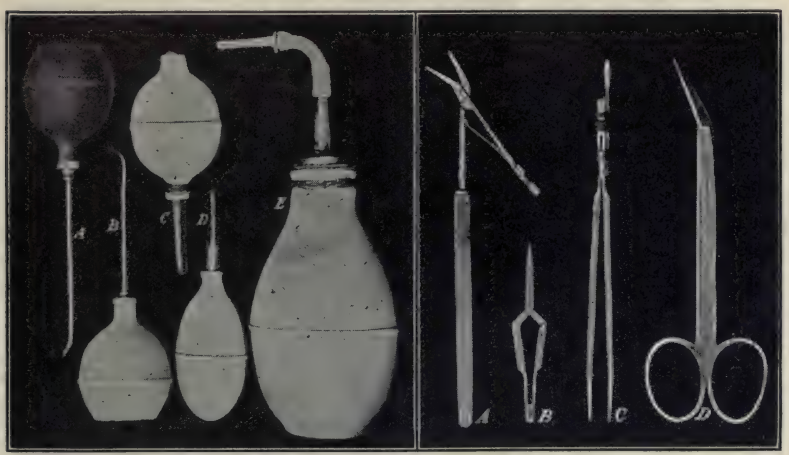


FIG. 16.—At right, *A*, scissors useful in removing small organs; *B*, self-closing forceps; *C*, forceps commonly used in emasculation with pin attached to the handle; *D*, scissors for severing large organs. At left, devices used in depollination of flowers; *A* and *B*, chip or water bulbs; *C*, water bulb with valve at bottom provided with celluloid ejector; *D*, old rubber bulb with glass tube inserted; *E*, "putty bulb" with attachment to give a small jet of water. (*After Babcock and Clausen*, 1918. *After Oliver*, 1910.)

Depollination with Water.—Oliver first used a garden hose in depollinating Grand Rapids lettuce. By cutting down the size of the opening with a smaller piece of rubber tubing a small jet of water was secured. After training this jet for a few seconds on

flowers which had just opened, no pollen remained. Small pieces of blotting paper were used to remove excess moisture and then pollen was applied. Fifteen flowers of lettuce were first crossed by this means and some seed was produced in each flower. The lettuce flowers and those of other closely related Compositæ close soon after pollination.

Certain small rubber-bulb syringes have been found satisfactory for field work. These are used to depollinate the flowers with water. For a complete description of artificial cross-pollination of alfalfa flowers the reader is referred to Oliver. In the flower to be used as the female, the anthers have already dehisced but can not perform the act of fertilization until the flower is tripped. To trip the flower and secure as small a percentage of pollination as possible is the aim. The technic of tripping and depollinating as well as the technic of crossing is a matter of practice. Oliver records that more than two-thirds of the alfalfa pollinations were successful by this method.

Summary of Technic of Crossing.—Some important features of the technic of crossing may be summarized.

1. Make a careful study of the structure of the flower before commencing operations. This may be done with the aid of a dissecting microscope.

2. Determine which flowers produce the larger, healthier seeds and which set seeds the more freely.

3. Learn the normal method of blooming of the flower, the period of receptivity of the pistil, and the length of time the pollen grains are capable of functioning.

4. Procure the necessary tools and see that these are of an efficient kind for the work to be undertaken.

5. Be careful not to injure the flowering parts any more than is necessary. Do not remove the surrounding flower parts, *i.e.*, petals in flowering plants, glumes of grasses, etc. unless necessary.

6. A few crosses well made are of much greater value than many pollinations carelessly executed.

CHAPTER VI

CLASSIFICATION AND INHERITANCE IN WHEAT

Studies of genetics have led to the adoption of a particular meaning which is understood when we speak of an inherited character. It is the final result of the interaction of many inherited factors plus the environment. The factors are the inheritance and the ultimate character is the manner of reaction under the special growing conditions to which the organism is subjected. What is inherited is the ability to react in a particular manner in a given place and not the character itself.

Genetic Classification.—Classification of cultivated varieties of crops is made in much the same manner as the botanical classification of wild species. With crops, there is as a rule considerable experimental evidence of genetic relationship. The ultimate aim of crop classification should be genetic in order that it may be of greatest value. Closeness of relationship as determined by the ease of crossing and the degree of sterility is frequently made the basis of species groups in some crops. In other crops no sterility is obtained in so-called species crosses. Only relatively stable characters which are not easily modified under different environmental conditions are considered of major classification value.

After placing cultivated crops in groups which are roughly analogous to botanical species, the next step is more clearly to separate different categories of a lower order of classification. These are the varieties. Varieties are not necessarily genetic entities but may be groups of similar forms which resemble each other more than individuals belonging to another variety. All members of a variety are similar to each other in major botanical characters.

Such a variety classification is of utmost importance. In the past the variety studies made in the United States by the different experiment stations or the federal Department of Agriculture have not always been comparable, as the same name has been used to refer to widely different varieties. More dependable results can only be obtained by the adoption of uniform variety names.

Classifications of some crops have recently been made and in the next few years these will be improved further. The general adoption of some standard variety classification is a necessity if work of different investigators in crops is to be correlated.

The central aim in crop improvement work is to find or produce improved forms which when grown by farmers will excel in quality, productivity, or ease of handling. It is a decided advantage if the improved form can be distinguished from the varieties commonly grown in the locality by some botanical or morphological character difference. Kanred (Jardine, 1917) wheat is an example of a new variety with such a character. This variety, which was developed at the Kansas station, belongs to the Crimean group of winter wheats. It gives larger yields on the average than Turkey or Kharkov selections and excels in resistance to black stem rust, *Puccinia graminis tritici*, and leaf rust, *Puccinia triticini*. Its beak, *i.e.*, the extension of the outer glume in the form of an awn point, is longer than in the common forms of Crimean winter wheat grown in Kansas. Marquis wheat, which is so widely grown as a spring wheat in the Northwest and Canada, differs in seed shape from other Fife wheats commonly grown in these sections. Forms belonging to the same variety may frequently exhibit differences in productivity and this may be the sole distinguishing character difference. Forms constantly differing from each other in one or more genetic factor differences which may be expressed as yield, quality, or disease resistance, or a minor botanical character and yet which belong to the same variety group, may be called strains. This is the lowest order of classification which can be adopted for seeded crops. With a self-fertilized crop the strain may also be a pure-line in the original sense as used by Johannsen. With cross-fertilized crops the strain may be relatively pure for some particular character and may be heterozygous for other characters.

Inheritance studies of many of our farm crops have been made. As crossing is the only means of inducing variation that can be carried out with success by the plant breeder, it becomes necessary to know how individual characters are inherited. It is true that yield is not a simple Mendelian character but is dependent on many inherited factors and their manner of reaction to the environment. At present, knowledge of inheritance may be used only as a guide in working with these characters. As a rule, the parental forms differ in botanical characters as well as in

yielding ability. A knowledge of the mode of inheritance of each of these characters is essential to the rapid purification of a cross.

It is not desirable in a text on plant breeding to outline variety classifications in very great detail. As a rule the crops student will be familiar with such classifications before studying crop improvement. It seems sufficient to indicate genetic relationship and to point out the characters which have been used.

Wheat Species Groups.—From the middle of the last century until the present time numerous crosses between wheat varieties and also between species groups have been made. Extensive crossing studies have led Tschermak (1914 *a,b*) to conclude that the genetic relationships in wheat are as represented in Table XV.

TABLE XV.—WHEAT SPECIES GROUPS

Group composition	Einkorn group	Emmer group	Spelt group
Stem species Spelt wheats	*T. aegilopoides*	*T. dicoccoides*	*T. spelta* wild form unknown
Cultivated forms Covered seed	*T. monococcum*	*T. dicoccum*	*T. spelta*
Cultivated forms Naked seed	Unknown	*T. turgidum* *T. polonicum* *T. durum*	*T. vulgare* *T. compactum*

Crosses reported by Tschermak between the einkorn and spelt-groups so far have proved wholly sterile, while the einkorns emmer crosses have proved only slightly fertile. Similar result. have been obtained by other investigators. The crosses between the covered emmer types and the naked and covered spelt forms or between covered and naked forms of the emmer group were partially fertile. Somewhat greater fertility was found in crosses between *T. polonicum* and the naked wheats of the spelt group, also between naked forms of the emmer group and the covered form of the spelt group. Some of the latter crosses seemed wholly fertile. Crosses between naked wheats proved wholly fertile.

Vilmorin (1880, 1883) concluded that spelt and common wheats belong to one group and *durum* and *turgidum* to another, for

crosses between any form in the first group with any form in the second group gave all cultivated forms of the spelt and emmer groups in later generations. Tschermak (1913) obtained similar results only from crossing solid and hollow stemmed varieties of the respective groups and only obtained *polonicum* forms when using *polonicum* as one of the parents.



FIG. 17.—Wild wheat from Palestine and the New Hybrid. Here is shown a spikelet of the true wild wheat and one of the hybrid forms. (*After Love and Craig*, 1919.)

T. dicoccoides was reported as being found wild as early as 1885. Aaronsohn (1910) found many wild forms of *T. dicoccoides* in Palestine. Love and Craig (1919*b*) have produced *T. dicoccoides* synthetically by crossing durum and common varieties, which indicates rather close genetic relationships between these forms. There seems no very good reason to the writers for

concluding that the cultivated emmer and spelt groups arose from different wild stem species. It is also essential to point out that all crosses between the cultivated naked emmer wheats with naked wheats belonging to the spelt group are not entirely fertile. Indications of partial sterility are generally apparent if the results are carefully analyzed (Kezer and Boyack, 1918) (Freeman, 1919) (Hayes and others, 1920).

Polonicum Crossed with Other Species.—Crosses between polonicum and other forms have been studied. Tschermak (1913), in a cross between *polonicum* and *vulgare*, explained the results by two main factor differences. The F_1 was of intermediate glume length and in F_2 *polonicum*, *durum*, and *vulgare* forms were obtained as well as intermediates. Pure *polonicum* was considered to contain two dominant factors in the homozygous condition; *durum*, one dominant factor pair in the homozygous condition; and the pure *vulgare* forms, both factors in the recessive condition.

Polonicum (Backhouse, 1918) crossed with *durum* or *turgidum* gave intermediate glume length in F_1 and segregation in F_2 in a ratio of 3 longs and intermediates to 1 short. Biffen (1916) and Backhouse in separate studies considered the factor for *polonicum* glume to inhibit chaff pubescence and color. In a cross between *durum* (Kubanka) with a *polonicum* variety, the F_2 segregated for glume length and hairy chaff. The short-glumed plants were in a ratio of 3 hairy to 1 smooth, while the long-glumed plants were difficult to classify for condition of chaff. Crosses of different long-glumed plants with other wheats showed that a part of these long-glumed wheats contained a genetic factor for hairy chaff. Results were explained on the hypothesis that the factor for long glume partially inhibited development of hairy chaff. Similar results were obtained by Biffen (1916), for inhibition of glume color by the *polonicum* factor for glume length.

Some Linkage Results in Wheat Crosses.—In crosses between the different species some evidences of linkage have been observed. In *turgidum-vulgare* crosses, Biffen (1905) obtained complete linkage of gray color of glumes with hairy chaff. Engledow (1914) crossed a black-glumed wheat obtained from a *turgidum*-fife cross with a rough-chaffed, white-glumed variety, Essex Rough Chaff. The ratio obtained in F_2 was explained on the basis of repulsion between the factors for black glume color

and those for hairy chaff on the 1:3:3:1 series. Kezer and Boyack (1918) obtained complete linkage of black and hairy chaff in a cross of black winter emmer with a smooth, white-chaffed winter wheat (*T. vulgare*). Freeman (1917) obtained



FIG. 18.—Upper group from left to right: Face and side views respectively of Iumillo durum (C.I., 1736), F_1 Iumillo × Marquis, and Marquis. The F_1 spikes are intermediate in density, have tipped awns and the outer glumes are keeled although not so strongly as Iumillo. Lower group, left to right, face and side views respectively of Emmer, Minn., 1165, F_1 Emmer × Marquis, and Marquis. The F_1 approaches the Emmer in some spike characters and has tipped awns.

some correlation between a high ratio of width to thickness of spike and hardness of grain in crosses between *T. durum* and *T. vulgare*. He considers, however, that numerous factors are necessary for the development of these characters.

Spike Density.—Compactness of spike, color of seed and chaff, texture of seed, and presence or absence of awns are frequently used in wheat variety classification.

Nilsson-Ehle (1911*b*), in crosses between compact and squarehead (mid-dense) wheats, obtained compact forms in F_1 and segregation into compact, mid-dense and lax in F_2. He explained the results by supposing the main factor differences to be as follows;

Swedish Binkel (compact) $CCL_1L_1L_2L_2$
Squarehead $ccl_1l_1l_2l_2$

The C factor was considered to inhibit the expression of the lengthening factors L_1 and L_2, and also to produce spikes with short internodes. While these factors gave a satisfactory explanation of his crosses Mayer Gmelin (1917) showed that they did not explain the production of compact spiked forms which he obtained from crosses of spelt (lax) and Essex Velvet Chaff, which is mid-dense. In F_2 generations grown from individual plants of a cross between white spring emmer and Marquis, studied at the Minnesota Experiment Station, a very common sort of segregation was from lax, keeled, speltlike wheats to compact, keelless, naked wheats. This might indicate that spelt wheats contain a compact factor which is prevented from expression by some other genetic factor.

Crosses between *T. compactum* and *T. vulgare* by Spillman (1909) and Gaines (1917) have shown one main factor difference for compactness. Parker (1914) made careful measurements of internode length in crosses of wheats belonging to *T. compactum* with those of *T. vulgare*. He was able to demonstrate segregation but found the condition very complex. Results of this nature have been satisfactorily explained by the multiple factor hypothesis. The number of factors involved cannot accurately be determined. Nilsson-Ehle, likewise, states that besides the main factor differences there are other minor factors which influence spike density and account for a wide range of homozygous forms.

Seed Characters.—Color of seed, which results from a brownish, red pigment in one of the bran layers (remains of nucellus) has been quite consistently used in variety classification. This is a plant character and not, therefore, immediately affected by pollination. Red is dominant over white and in the second

generation a ratio of 3 red-seeded plants to 1 white-seeded plant is often obtained. Nilsson-Ehle (1911*b*) was the first writer who reported crosses which in F_2 gave 15 to 1 or 63 to 1 ratios of red- and white-seeded plants. The Howards (1912), in India, have obtained 63:1 ratios in crosses of American Club with pure lines of Indian wheats, and Gaines (1917) in Washington, has obtained similar results from a cross between Bluestem (red seed) and Brown's Glory (white club wheat). Nilsson-Ehle obtained a ratio of 15 red-seeded plants to 1 white-seeded plant from a cross of two red-seeded varieties. The inheritance of this seed color has been explained by one or more Mendelian factors, each when present giving red and when absent white. The factors are separately inherited, each when homozygous producing somewhat darker color than when heterozygous. They are also cumulative, two factors giving a darker color on the average than one of these factors alone. It is impossible, by inspection, to determine how many factors are responsible for a particular varietal seed color.

Texture of seed has also been used in varietal classification and is a character which determines to some extent the market class in which the variety will be placed. Biffen (1916) found immediate effect of pollination in a cross of Rivet, a hard-seeded *turgidum* with pollen from a soft Polish variety. The F_1 generation plants produced hard seed and the F_2 segregated into hard- and soft-seeded plants in a ratio of 3:1. The Howards (1915) obtained an intermediate condition in F_1 plants and a 1:2:1 ratio in F_2 in crosses between hard- and soft-seeded strains. Freeman (1918) crossed hard-seeded durums with *T. vulgare*, variety Sonora, a soft-seeded wheat. The F_1 plants produced hard, intermediate, and soft seeds. The hard seeds of the F_1 tended to give more hard-seeded plants in F_2, and the soft-seeded tended to give more soft-seeded plants. Freeman carried the study through F_4. He explained his results on the basis of two factors for starchiness, each inherited independently. He supposed each to produce half as much soft starch when heterozygous as when homozygous. As the endosperm is the result of the fusion of two polar nuclei with one of the male generative

FIG. 19.—Representative spikes of F_3 families of the cross between Durum and Marquis. Upper 4 groups, F_3 families which were classified as durums. Note that they represent all types of spike density. Lower left, spikes of an awnless F_3 Emmer family. Lower right, four spikes of an F_3 plant which resembled common wheat in spike shape and which proved rust resistant.



FIG. 19.

nuclei, there may be a range of from 0 to 6 factors for starchiness of the endosperm. This assumption was shown to explain results quite satisfactorily. The above starchiness is believed by Freeman to be quite different from the well-known "yellow berry" of wheat. Numerous workers have shown that varieties and strains differ widely in the amount of "yellow berry" when grown under the same environmental conditions. Texture of seed is, however, a character which is quite easily modified by unfavorable environmental conditions.

Chaff Characters.—There are a number of different intensities of the chaff color. In some cases a deep brownish red color is present, in other cases a light brownish-red, and frequently the outer glumes have dark brownish red striations on a slightly colored or colorless background. Biffen (1905) studied crosses between so-called red and colorless and obtained red or reddish color in F_1 and a 3:1 segregation of colored to colorless in F_2. Kezer and Boyack (1918), in winter wheat crosses in which the parents differed in chaff color, obtained intermediate color in F_1 and segregation in a 3:1 ratio in F_2. Simple ratios in varietal crosses have been reported by others for this color character. As there are different intensities which are quite uniform in inheritance it seems reasonable to conclude that there are different factors in different varieties for brownish-red color. In a *durum-vulgare* cross, Love and Craig (1918a) obtained in F_2 an indication of a 15:1 ratio for brownish red and colorless chaff.

Besides the chaff colors there are awn colors. The Howards (1915), in India, obtained a ratio in F_2 of 3.45 black-awned to 1 colorless in a cross between Indian wheats.

Hairy chaff is a varietal character of considerable classification value. The Howards have made extensive studies of this character. Under linkage relations a number of cases were given in which hairy chaff was correlated with glume color. Henkemeyer (1915) reports different crosses, one in which hairy chaff is correlated with white chaff and another in which these characters are independently inherited. This leads one to suspect that there are two kinds, either of hairy chaff or of chaff color. The Howards have been able to demonstrate two kinds of hairs on the glumes of Rivet wheat. Two Indian varieties were likewise studied. Each produced hairy chaff, but differed in the sort of hairs produced. In crosses between these varieties, ratios of 15 pubescent to 1 smooth were obtained in F_2.

Presence or Absence of Beards.—Wheats have been classified as bearded and awnless but this is not genetically correct. The awn is an extension of the flowering glume. The common wheats, like Marquis and Bluestem, are not truly awnless for there is a short extension of the awn particularly in the spikelets at the top of the spike. Three to one ratios have generally been obtained in crosses between bearded and so-called awnless (tip-awned) wheats. The Howards (1915) have carefully worked out the inheritance of these characters. They have explained results by supposing two factors, *A* and *B*, to be present in a homozygous condition in bearded wheats. They have found two kinds of very short-awned wheats, one like the tip-awned Marquis or Bluestem, and the other with somewhat longer tip awns. Each of these varieties was found to contain one of the factors *A* or *B* in a homozygous condition. In crossing a tip-awned wheat like Marquis with bearded varieties, the F_1 generation, as a rule, shows an extension of the tip awns and it is frequently possible to separate these F_1 plants from the tip-awned parent. In crossing bearded with true beardless, the F_1 is apparently beardless and there is a range in F_2 from completely bearded to awnless. Fully bearded plants breed true for this character.

Inheritance of Disease Resistance.—Biffen (1907a, 1912, 1917) has found that the inheritance of host reaction to stripe rust, *Puccinia glumarum*, is a simple Mendelian character. Susceptibility is dominant over resistance and in F_2, ratios of 3 susceptible to 1 resistant are obtained. Nilsson-Ehle (1911b) in a similar study found the F_1 generation resembled the susceptible parent in some cases, the resistant in others, and was intermediate in still others. Complex segregation for resistant *versus* susceptible forms was obtained in later generations. Results were explained on the multiple factor basis.

Studies by Stakman and others (1919) have shown the probable reason for conflicting reports regarding inheritance of resistance to black stem rust of wheat, *Puccinia graminis tritici*. They have demonstrated the fact that there are a number of biological or racial forms of rust roughly analogous to pure lines. These forms can only be differentiated surely by their specific reaction to pure-line wheat varieties. Studies of their constancy indicate that they are not easily modified, *i.e.*, that the parasitic reaction of each form is constant. At the Minnesota Station (Hayes and others, 1920) studies of inheritance of resistance were made in

crosses between resistant emmers and durums with susceptible Marquis. A single rust form was used in making the artificial epidemic. The durum-Marquis crosses were as susceptible as Marquis in F_1. Using white spring emmer as the resistant parent, the F_1 was resistant, though not so resistant as the emmer parent. Segregation for resistance and botanical characters was studied in later generations. Some linkage in transmission was apparent, for while it was quite easy to obtain resistant emmer or durum

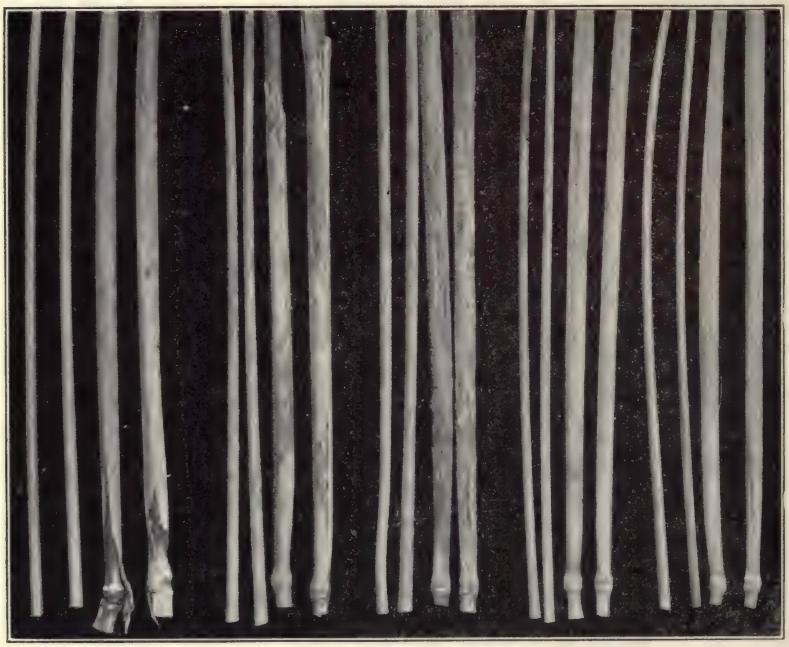


FIG. 20.—Resistance of parents and crosses to a strain of stem rust. From left to right: Culms of resistant Durum wheat; F_1 of Durum × Marquis, susceptible;, Marquis, susceptible; F_1 of Emmer, Minn. 1165 × Marquis, as resistant as the Durum varieties; Emmer, Minn. 1165, a very resistant variety.

plants it was much more difficult to obtain resistant common wheats. In an examination of more than 20,000 F_3 plants, a few with *vulgare* spike characters and resistance were obtained. Resistant plants resembling emmer, durum, and common wheats were also proved resistant by greenhouse inoculation studies.

Gaines (1918, 1920) has studied the inheritance of resistance of wheats to bunt (*Tilletia tritici*). It is estimated that this

disease causes an annual decrease of 15 per cent. in the yield of winter wheat in the States of Washington, Oregon, and Idaho.

The method used in studying bunt resistance was to blacken the seed with smut spores just before planting and then sow the strains and crosses in rows in such a way that each plant could be individually examined.

Studies of inheritance were made in crosses of Turkey × Florence and Turkey × Hybrid 128. Hybrid 128 is a prolific, winter-hardy, stiff-strawed wheat of much commercial value but it is very susceptible to bunt. Turkey does not yield as well as Hybrid 128, has weak straw, and shatters considerably. It is highly resistant to bunt. Florence is an Australian spring wheat which is highly resistant to bunt.

The results presented by Gaines show very clearly that resistance to bunt is an inherited character. However, several factors are necessary to explain the sort of segregation obtained. The F_2 of the cross between Florence and Turkey showed transgressive segregation. In F_3, 171 families were grown from individual F_2 plants. Of these, 72 were immune while 50 families produced over 80 per cent. of bunt. The Turkey and Florence parents under the same conditions produced an average of 4.6 per cent. of infected plants. This shows that the factors for resistance in the Florence and Turkey varieties are not identical.

In the cross between Turkey and Hybrid 128 no segregates were obtained with a higher degree of resistance than the Turkey parent. It was found possible to produce resistant strains of any morphological type desired.

Inheritance of Other Characters.—Nilsson-Ehle (1911*c*, 1912) has shown that winter-hardiness is inherited in much the same manner as other characters. Segregation occurs in F_2 and types can be produced in later generations which are homozygous for different degrees of winter-hardiness. Crosses made (Hayes and Garber, 1919) in 1902 between hardy Odessa winter wheat and Turkey varieties were bred for several years by continuous selection methods. Odessa is a late maturing variety and does not give a high yield in Minnesota. Turkey is a desirable winter wheat in many sections but it lacks hardiness under Minnesota conditions. Two early maturing wheats, Minhardi and Minturki, have been produced from the cross between Turkey and Odessa. These new varieties excel in winter-hardiness and yield.

The Howards (1915) state that standing power is due to a combination of a strong root system and stiff straw and report segregation and recombination in a cross between two varieties, each of which contained one character and lacked the other. It was impossible to determine the factors involved. Spillman (1909) made a cross between a winter wheat with weak straw and spring wheat with stiff straw and obtained in later generation a winter wheat with stiff straw. Examples of inheritance of other similar characters could be given. It is reasonable to conclude that those growth characters which determine the productive capabilities of each variety are inherited in the same manner as botanical characters. They are due, generally, to the interaction of numerous factors which are dependent for their full expression on favorable environmental conditions.

CHAPTER VII

CLASSIFICATION AND INHERITANCE OF SMALL GRAINS OTHER THAN WHEAT

In the cases of barley and oats quite usable classifications have been proposed. The general adoption of such classification schemes is desirable for often great confusion results from the incorrect use of varietal names. Classification schemes can not be given in detail in a plant breeding text. It seems sufficient here to point out the genetic relationship between wild and cultivated species and to give the major so-called species groups for the various crops. The more important botanical and agronomic characters which are commonly used in varietal classification have also been mentioned. As crossing must frequently be resorted to as a means of improving small grains, the student should have a working knowledge of the known facts of inheritance with respect to particular characters.

CLASSIFICATION AND INHERITANCE IN OATS

A workable classification of cultivated American oat varieties and the basic wild species has been made by Etheridge (1917). The following outline of species groups is taken from his publication;

A. Kernel loose within the surrounding hull; lemma and glumes alike in texture..... *Avena nuda.*

AA. Kernel firmly clasped by the hull; lemma and glumes different in texture.

B. Upper grains persistent to their rachillas..... *Avena sterilis.*

BB. Upper grains easily separating from their rachillas.

C. Lemma bearing as teeth or awn points.

D. Lemma with four teeth or awn points. *Avena abyssinica.*

DD. Lemma with two teeth or awn points.

E. Lemma elongate, lanceolate, with distinct awn points..... *Avena strigosa.*

EE. Lemma short, abrupt, blunt, rather toothed than awn-pointed..... *Avena brevis.*

CC. Lemma without teeth or awn points.
D. Basilar connections of the grains articulate
Avena fatua.
DD. Basilar connections of the grains solidified.
E. Panicles roughly equilateral, spreading.
Avena sativa.
EE. Panicles unilateral, appressed.
Avena sativa orientalis.

Crosses Between Avena fatua and A. sativa.—It is generally accepted that *fatua* is the stem species from which *A. sativa* and *A. sativa orientalis* originated. Tschermak (1914) has made extensive crosses and obtained nearly complete fertility in crosses between *fatua* and *sativa* forms. Surface (1916) has found a number of characters which in crosses between *fatua* and *sativa* are associated with the fatua base—(1) heavy awn on lower grain, (2) awn on upper grain, (3) *fatua* base on upper grain, (4) pubescence on rachilla of lower grain and upper grain, (5) pubescence on all sides of the base of lower grain and pubescence on the upper grain.

Origin of the Cultivated Varieties of A. sterilis.—Norton (1907) pointed out that the red oats grown in southern United States without doubt descended from *A. sterilis* of the Mediterranean region. Trabut (1914) gives quite convincing evidence that the cultivated oats of the Mediterranean region have been obtained from a wild *A. sterilis*, which is still quite common. It is of interest to the student of plant breeding that the cultivated oats grown in the warmer regions of the United States descended from warm-climate ancestors. The value of this group of oats for the southern United States has clearly been shown by Warburton (1914).

Differences in Awn Development.—Varieties of oats differ in the presence or absence of awns and in the degree of awn

FIG. 21.

1. Branch of oat panicle.
2. Spikelet, showing tertiary floret just after blooming—*a*, primary floret.
3. Spikelet, showing flower parts—*a*, outer glume; *b*, flowering glume; *c*, palea; *d*, lodicules; *e*, anther; *f*, stigma; *g*, secondary floret; *h*, awn.
4. Outer parts removed, showing sexual organs.
5. Longitudinal section ovary.
6. Anther.
7. Showing outer and flowering glume of lower spikelet removed—*a*, lodicules, and sexual organs.

Size: 1, 2, about *n*; 3, about 2*n*; 4, 5, 6, greatly enlarged; 7, about 2*n*.

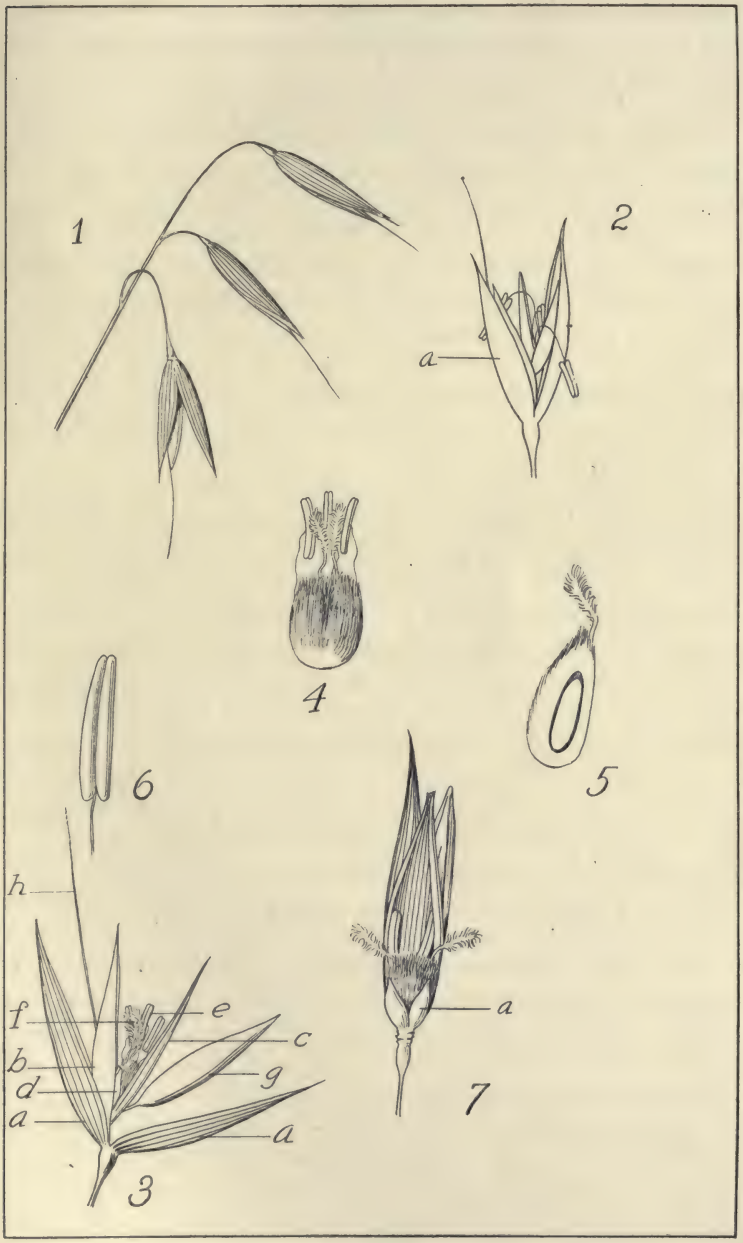


FIG. 21.

development. Nilsson-Ehle (1911a) first used the hypothesis that the yellow gene inhibited the development of awns. This hypothesis was substantiated by careful experiments. A number of crosses betwen *Avena fatua*, hairy awns on both grains, with early oats belonging to the *Avena sativa* group have been studied. Using Sixty Day with yellow grains as the awnless parent, Love and Craig (1918c) observed the F_1 to have the lower grain often awned but the upper grain awnless. They concluded that the yellow factor inhibited the complete development of awns. In a similar cross, Surface (1916) obtained like results in F_1 and concluded that one main factor difference was necessary to explain the results. Modifying factors were involved which affected the degree of development of awns. No significant evidence was found that the yellow gene inhibited the development of awns.

Fraser (1919) has studied a cross between an awnless Sixty Day and Burt, the latter being a variety of the *Avena sterilis* group. The Sixty Day parent produced bright yellow grains with no awns. The Burt parent usually produced awns on the lower grains and frequently on the upper but they show weak development. Fraser classified awns as strong, intermediate, and weak. The strong awn is twisted at the base and has a sharp bend about three eighths of the way from the base to the tip. It is also stiff and long. The intermediate awn lacks the bend of the strong awn and is less stiff. It is generally twisted at the base and is often curved. The weak awns vary greatly from almost imperceptible structures to weakly developed ones. The F_1 plants of Burt $\times$ Sixty Day were practically awnless. In F_2 there was a ratio of fully awned (awned like Burt or with awns more completely developed) to awnless and partly awned of 1 : 3. The fully awned bred true in later generations. Results substantiated the hypothesis that Sixty Day carried a factor for awning which was inhibited from development by the yellow factor.

Color of Grain and Straw.—Color of the lemma when ripe is a character which is easily affected by environment. Weather conditions at ripening are important and greatly modify the expression of inheritance of these color characters. With bright sunshine a deeper color is developed than in wet, cloudy weather. Black or yellow grained varieties under unfavorable environmental conditions are much less intensely colored. The stage of matu-

rity at which the grain is harvested or weathering after harvesting may also modify these color characters.

The color of the lemma of oats has been classified as black, brownish red, gray, yellow, and white. Different varieties, likewise, exhibit different intensities in the development of a particular color. In some crosses between black and white a ratio of 15 blacks to 1 white was obtained in F_2 (Nilsson-Ehle, 1909), while the majority of crosses show 3:1 ratios (Nilsson-Ehle, 1909), (Gaines, 1917). The simplest explanation is that each color character is due to one or more factors, each factor when heterozygous causing partial or complete development of the character.

Results of crosses show that yellow is dominant over white or partially so. There are, however, two yellow factors each independently inherited. In a cross between Burt, which produces yellowish red seeds, and Sixty Day, which produces yellow seeds, Frazer (1919) obtained a ratio of 48 red, 15 yellow, and 1 white in F_2. These results may be explained by supposing Burt to carry two color factors, R for red and Y for yellow, and Sixty Day one factor, Y^1 for yellow. Apparently R produces reds either when associated with Y or Y^1 or when alone.

Gray is epistatic to yellow (Nilsson-Ehle, 1909) (Surface, 1916) (Love and Craig, 1918*c*) but hypostatic to black, while black is epistatic to all other colors so far as determined. It has been tested for gray, yellow, and white but not for brownish red. As a rule the intensity of color is not so great when a factor for a particular color is heterozygous as when homozygous.

The inheritance of a reddish straw color has been shown by Pridham (1916) to behave as a simple Mendelian monohybrid.

Hulled versus Hull-less.—The hull-less condition has been made the basis of one of the species groups, *Avena nuda*. Numerous crosses between hulled and hull-less forms have given like results. All investigators of these crosses have obtained an intermediate condition in F_1, with both kinds of grains, hulled and hull-less, borne in the same panicle. Ratios in F_2 of 1 of each of the hulled and hull-less forms to 2 heterozygotes have been obtained. The hulled and hull-less types breed true while the intermediates again segregate. Love and McRostie (1919) have found considerable variation in the percentage of hulled and hull-less seeds in different panicles of the same cross. Consistent correlation was obtained between the percentage of hulled

grains on heterozygous F_2 plants and that of hulled grains on heterozygous F_3 plants. Some heterozygous F_2 plants with low percentages of hulled grains gave heterozygous progeny with correspondingly low percentages. A similar behavior was obtained in the progeny of heterozygous plants with high percentages of hulled grains, while plants with intermediate percentages of hulled grains gave heterozygous progeny with low, intermediate, and high percentages in different plants. This suggests the presence of a factor which affects the percentage of hulled and hull-less grains of heterozygous plants.

Pubescence.—Cultivated varieties of oats differ in the amount and in the presence and absence of basal hairs on each side of the callus. In some crosses only one factor is involved, in others two factors. In some crosses between parents which have different degrees of pubescence there is an increase in the number of basal hairs, and forms are obtained in F_2 which have more pubescence than either parent, likewise forms which lack pubescence. Certain wild forms of *Avena fatua* carry two independently inherited factors for pubescence (see Surface, 1916; Zinn and Surface, 1917; Nilsson-Ehle, 1908; Love and Craig, 1918*c*).

Characters of Base of Lower Grain.—In wild forms of *Avena fatua* and cultivated forms of *Avena sterilis* there is a distinct articulation at the base of the lower grain. According to Surface (1916) this causes wild oats to shatter while in cultivated races of *sativa* the grains are not easily separated from their base and do not ordinarily shatter. The F_1 generation of a cross between *A. fatua* and Kherson was intermediate as regards the base of the lower grain, but nearer the cultivated form, while the upper grain had a base similar to the cultivated parent. Segregation in F_2 gave a ratio of wild, intermediate, and cultivated of 1 : 2 : 1. This leads to the assumption of a single factor difference which separates cultivated and wild in the form of the base. As has been mentioned, there is strong association of many other characters and the wild form of the base. Love and Craig (1918*c*) found an indication of a single factor difference for the presence and absence of basal articulation but found that the yellow factor inhibited the development of the wild or articulated base.

Avena sterilis differs from other oat species in having the upper grain persistent to the rachilla. The base of the lower grain resembles *A. fatua* in its articulation. In crosses between Burt, belonging to *A. sterilis*, and Sixty Day, the F_1 was intermediate

and in F_2 the articulated basal types could easily be determined. These occurred in a close approximation of the ratio of 1 articulated base to 3 of the intermediate and *sativa* types (Fraser, 1919).

Open versus Side Panicle.—Nilsson (1901) has used panicle types and seed colors as a chief means of classification. The distinction between the side and the open panicle is easily made, but the various transitional open panicled forms are not easily used in differentiation. Nilsson-Ehle (1908) has explained crosses between an open-panicled and a side-panicled variety on the basis of two main factor differences. Either factor when homozygous or heterozygous produces open panicles. When both factors are homozygous a variety with an open panicle and drooping branches is obtained. When the factors are absent a side panicle results. From crossing two open-panicled forms, 9-side forms were obtained out of a total of 112 plants. These side-panicled plants bred true while of the 103 open-panicled plants, 24 again segregated giving both open- and side-panicled forms. The parental varieties have panicles with erect branches while a part of the open-panicled segregates have drooping branches.

Resistance to Rust.—Parker (1918) studied varietal resistance of oats to stem rust, *Puccinia graminis avenæ* Erikss. and Henn. and to crown rust, *Puccinia lolii avenæ* McAlpine. Crown rust is a serious disease in the South while stem rust is more common in the North. Several varieties of the red oat group of *A. sterilis* including Burt, proved resistant to crown rust, while certain side oat strains of *A. sativa orientalis* belonging to the White Russian group proved resistant to stem rust.

Studies, of the inheritance of resistance to crown rust under greenhouse conditions, of crosses of Burt with Sixty Day, *A. sativa*, showed segregation in F_2. Susceptible and resistant plants, as well as various intermediates, were obtained (Parker, 1920).

A study of the inheritance of resistance to stem rust has been made at the Minnesota Station (Garber, 1921). F_1, F_2, and F_3 crosses of resistant White Russian with two susceptible varieties of *A. sativa*, Victory and Minota, have been grown. The preliminary results show that for these crosses resistance is a dominant character, the ratio in F_2 of resistant and susceptible plants approximating 3 : 1. Susceptible F_2 plants bred true to

susceptibility in F_3, while resistant F_2 plants were of two kinds: (1) those which produced only resistant progeny and (2) those which segregated, both resistant and susceptible plants being obtained.

Size Characters.—Nilsson-Ehle (1908) made numerous studies of inheritance of size characters. In a cross between two *sativa* varieties which differ in height, transgressive segregation occurred in F_2. Forms were selected and the studies continued

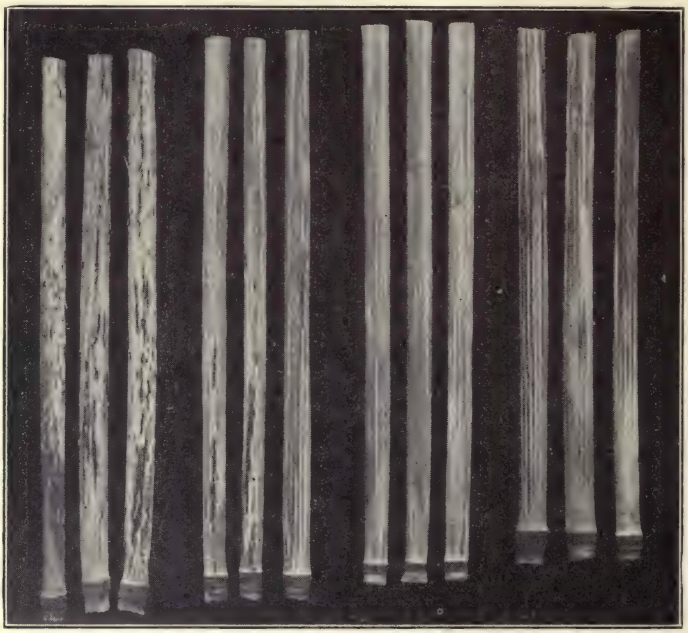


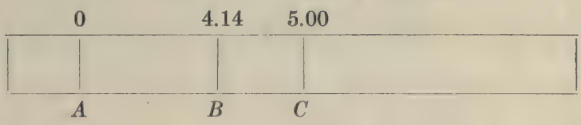
FIG. 22.—Culms of resistant and susceptible varieties of oats. From left to right: Victory, susceptible to stem rust; a susceptible F_2 plant of Victory × White Russian; a resistant F_2 plant of Victory × White Russian; resistant White Russian.

through F_4 and F_5. Segregation was of a complex nature. Transgressive segregation also occurred in crosses involving leaf breadth, kernel size, and number of florets to the spikelet. The results were explained on the multiple factor hypothesis, but the actual factors involved could not easily be determined. Maturity may be considered under this heading, for it behaves in a similar manner. From crossing early and later maturing oats, Caporn (1918) obtained intermediate maturity in F_1 and segregation in F_2. The author suggests that three factors will quite satis-

factorily explain the results. Nilsson-Ehle obtained transgressive segregation in F_2 in a cross between medium early and late maturing varieties. Progeny from 112 F_2 plants were grown in F_3. Of these 112 plants, 98 gave segregating progeny for maturity and 14 seemed to be homozygous. Homozygous forms were obtained which were earlier than the early parent and others which were later than the late parent.

Linkage of Characters.—Association of numerous characters in inheritance has been mentioned in the discussion of crosses between the wild *A. fatua* and cultivated varieties of *A. sativa*. Aside from the general characters mentioned, linkage has been found between the factor for black color of the lemma and one of the factors for pubescence.

In crosses between Burt, *A. sterilis*, and Sixty Day, *A. sativa*, Fraser (1919) has found that the factors for the articulated base of the lower grain, the awned condition, and the production of medium basal hairs were linked in inheritance. In the following diagram *A* represents the factor for awning, *B* for Burt base, and *C* a factor for the production of medium basal hairs.



The percentages of cross-overs were determined for F_2 and F_3. As has been pointed out, each of the characters depends on a single factor for its development. Five per cent. of cross-overs occurred between the factors for awning and basal hairs; 4.14 per cent. between awning and the factor for Burt base, and 1.79 per cent. between Burt base and basal hairs.

False Wild Oats.—False wild oats differ from the cultivated varieties in the production of heavier awns, in heavy pubescence, and in the basal articulation. False wild oats resembling cultivated varieties in color and panicle characters have been found by numerous investigators. Nilsson-Ehle (1911*a*) has reported false wild oats in eleven pure-line selections and in two commercial varieties belonging either to *A. sativa* or *A. sativa orientalis*. A heterozygous false wild form was found in the second generation of a cross between *sativa* varieties. It gave a ratio of 1 cultivated, 2 heterozygous to 1 false wild form. The heterozy-

gous forms are less heavily awned than the false wild and have the *fatua* type of callus only on the lower grain. Considerable difference of opinion is held regarding the cause of the production of false wild oats. Whether they originate as a loss mutation or through hybridization or both is not yet determined. Some evidence for hybridization and some for mutation has been obtained.

CLASSIFICATION AND INHERITANCE IN BARLEY

Students of barley classification have frequently used density and sterility of the lateral florets as chief means of separating the larger cultivated groups. While density is quite a stable character, there are gradations in the length of the internode from the very lax to the very dense spikes without any clear-cut differentiation between the mid-dense and mid-lax groups. While density is an important character by means of which to differentiate forms, it is not very usable as a chief means of group classification. Harlan (1918) has made an interesting review of barley classification studies and has presented a new grouping in which species are made on the basis of fertility of the lateral florets. The following key is taken from Harlan's paper:

All spikelets fertile (six-rowed barley)
Lemmas of all florets awned or hooded..... *Hordeum vulgare* L.
Lemmas of lateral florets without awns or hoods... *H. intermedium* Kcke.

Only the central spikelets fertile (two-rowed barley)
Lateral spikelets consisting of outer glumes, lemma, palea, rachilla, and usually rudiments of sexual organs..... *H. distichon* L.

Lateral spikelets reduced usually to only the outer glumes and rachilla, rarely more than one flowering glume present and never rudiments of sexual organs..... *H. deficiens* Steud.

There are several contrasting characters by means of which variety groups are made. Harlan has used the following to differentiate the variety groups belonging to each of the four species groups:

Seeds hulled; seeds naked.
Lemmas awned; lemmas hooded.
Seeds white, blue, purple; seeds black.

In classifying the cultivated varieties of barleys, the density of the spike, its shape, and the appearance of the awns as well as the color of the seed, have been used. Smooth-awned varieties are being produced and it is only a question of time before nearly all awned varieties will be represented by both the rough and smooth-awned forms.

Species Crosses.—Two general results have been obtained from crossing two- and six-rowed varieties. The most frequent result is an intermediate condition in F_1 in which the lateral florets are awned, but produce little or no fruitfulness. In F_2 a 1 : 2 : 1 ratio of six-rowed, intermediate, and two-rowed forms is obtained. Six-rowed and two-rowed forms breed true to these respective characters in later generations. Results of this nature can easily be explained on a single main factor difference (Biffen, 1907*b*; Gaines, 1917).

The *intermedium* barleys have generally been considered to be of hybrid origin. A coöperative study carried on at the Minnesota Experiment Station has shown the probable origin of some *intermedium* forms (Harlan and Hayes 1920). In a cross between Manchuria, a six-rowed barley, and Svanhals, a two-rowed variety, the F_1 was slightly fruitful and produced intermediate developed awns on the lateral florets. In F_2 a wide range of forms was obtained. The genetic nature of the F_2 plants was determined by growing seed of each in F_3. From the F_3 results it was possible to classify F_2 plants as follows:

1. Those that bred true for the six-rowed character.
2. Those that segregated, giving six-rowed, awned intermediate forms with very high fruitfulness of the lateral florets and *intermedium* forms in a 1 : 2 : 1 ratio.
3. *Intermedium* forms that bred true, giving few or no awns on lateral florets and producing approximately 50 per cent. of barren lateral florets.
4. Those that gave all forms as in F_2.
5. Those that produced intermediates and two-rowed types.
6. Those that produced six-rowed, awned intermediates with little or no fruitfulness in the lateral florets and two-rowed forms in a 1:2:1 ratio.
7. Those that bred true for the two-rowed condition.

Results were accurately explained by considering the Manchuria parent to contain two factors, one for six-rowed and one for *intermedium*, which was hypostatic to the six-rowed factor. It

was thought possible that minor modifying factors were sometimes present which influenced the degree of fruitfulness of the lateral florets.



FIG. 23.—Individual spikes of F_2 generation of cross of Svanhals × Manchuria representing phenotypic progeny classes in which the lemmas of the lateral florets are rounded and awnless. From left to right: The two-rowed class which will breed true in F_3; low fertility class which will give two-rowed, low fertility and *intermedium* in F_3; *intermedium* which will breed true for intermedium habit in F_3. (*After Harlan and Hayes*, 1920.)

Crosses between *intermedium* and six-rowed forms gave intermediates of high fruitfulness in F_1 and a ratio of six-rowed to intermediates in F_2 which indicated a single factor difference. *Intermedium* forms crossed with two-rowed gave awnless forms

with very low fruitfulness in F_1 and a ratio indicating one main factor difference in F_2.



FIG. 24.—Individual spikes of F_2 generation of cross of Svanhals × Manchuria representing the phenotypic progeny classes in which lateral florets bear awns. From left to right: Low fertility awned plant which will give all classes of segregates in F_3 as in F_2; high fertility awned which will segregate into *intermedium*, high fertility awned and six-rowed in F_3; six-rowed which will breed true in F_3. (*After Harlan and Hayes*, 1920.)

Biffen (1907b) found the sexless condition dominant in a cross between *deficiens* and two-rowed. Results from an F_2 generation of a similar cross grown at the Minnesota station indicate that it is almost impossible to separate *deficiens*, two-rowed, and inter-

mediates by inspection. No other strains except the parental forms and various grades of intermediates were obtained.

These facts indicate that a classification made on the basis of sterility for the species groups is reliable.

Simple Mendelian Characters.—So far as studied there are several barley characters which can be grouped according to their inheritance and which give simple Mendelian ratios. These are summarized in Table XVI.

TABLE XVI.—BARLEY CHARACTERS WHICH SHOW SIMPLE MENDELIAN INHERITANCE

Character differences	F_1	F_2	Authority
Awnless *vs.* Hooded....	Awnless	3 awnless to 1 hooded	Tschermak (1901)
Hooded *vs.* Awned.....	Intermediate hooded	3 hooded to 1 awned	Tschermak (1901) Thatcher (1912)
Rough *vs.* Smooth Awn	Toothed	3 toothed to 1 smooth	Harlan (1920)
Black Palea *vs.* Colorless	Black	3 black to 1 colorless	Tschermak (1901) Biffen (1907b)
Purple Palea *vs.* Colorless	Purple	3 purple to 1 white	Biffen (1907b)
Hulled *vs.* Naked.....	Hulled	3 hulled to 1 naked	Thatcher (1912) Gaines (1917)

A study of inheritance in barley was made at the Minnesota Station in coöperation with the Office of Cereal Investigations, United States Department of Agriculture. A cross of Virginia Hooded, a six-rowed, hulled, hooded, colorless barley, with Jet, a two-rowed, naked, awned, black-glumed barley was studied. In this cross there was apparently only one factor difference between two-rowed and six-rowed and the intermediate forms were classed as two-rowed, although they could be differentiated from true two-rowed forms by the presence of awns on the lateral florets. The results showed that these four factor pairs were independently inherited and gave a close approximation to expectation. Crosses differing by four independently inherited, sharply differentiated factor pairs have not been frequently presented, therefore the results are of some interest. They are as follows:

TABLE XVII.—INHERITANCE OF 4 INDEPENDENTLY INHERITED MENDELIAN CHARACTERS

	EXPECTATION	OBTAINED
Hooded, two-rowed, black, hulled	129.0	113
Hooded, two-rowed, black, naked	43.0	43
Hooded, two-rowed, white, hulled	43.0	42
Hooded, six-rowed, black, hulled	43.0	56
Bearded, two-rowed, black, hulled	43.0	45
Hooded, two-rowed, white, naked	14.3	14
Hooded, six-rowed, black, naked	14.3	15
Hooded, six-rowed, white, hulled	14.3	14
Bearded, two-rowed, black, naked	14.3	14
Bearded, two-rowed, white, hulled	14.3	17
Bearded, six-rowed, black, hulled	14.3	14
Hooded, six-rowed, white, naked	4.8	4
Bearded, two-rowed, white, naked	4.8	6
Bearded, six-rowed, black, naked	4.8	6
Bearded, six-rowed, white, hulled	4.8	4
Bearded, two-rowed, white, naked	1.6	1
Totals	407.6	408

Biffen found that there was a correlation between the black color of the grain and the color of the palea in barley crosses. Two Japanese workers, Miyazawa (1918) and So (1918), independently, have found xenia when white-seeded varieties were pollinated with black-seeded strains.

Winter versus Spring Habit.—Fruwirth (1909) lists spring forms as dominant over winter as the usual mode of inheritance. Gaines (1917) has obtained some winter forms from spring crosses. In one cross he obtained 18.75 per cent. winter plants and 81.25 per cent. spring plants in F_2. Results were explained by supposing one variety to carry a factor for winter habit which was prevented from expression by an inhibitory factor. The other parent was considered to lack both factors.

Density of the Spike.—Biffen (1907b) studied two crosses between barleys which differ in the length of internode of the spike. He found the F_1 nearly as lax as the nutans parent and obtained curves in F_2 which indicated that there was one main factor difference. Some of the more dense F_2 segregates were tested in F_3. From 65 plants so tested, 55 proved homozygous for the dense condition.

A biometrical study of inheritance of density[1] in a number of

[1] The average length of internode in the middle of the spike was obtained by measuring the length of 10 central internodes, in millimeters, and pointing off one place.

crosses has been made at the Minnesota Station in coöperation with the Office of Cereal Investigations (Hayes and Harlan, 1920). In a cross between Manchuria and Svanhals, the F_1 proved nearly as dense as the Svanhals parent. F_2 and F_3 results showed these parents to differ by one main density factor.

Pyramidatum, a dense, six-rowed form, was crossed with Jet, a lax two-rowed form. The average length of internode of Pyramidatum was 2.11 mm., of Jet 3.92 mm., of the F_1, 2.86 mm. of F_2, 3.01 mm. All forms were grown the same year. The F_2 generation gave a continuous range of variability which reached beyond the modal classes of the parents. Forms bred true in F_3 to densities which were not widely different from those of the parents but no homozygous intermediates were obtained. Apparently these parental types differ by a single main density factor. There are other minor factors which influence the expression of density. One such minor factor difference is known. Some barleys have a slight progressive increase in internode length from the base to the tip of the spike, in others all internodes have nearly the same average length.

Different results were obtained in a cross between Hanna, a lax, two-rowed variety, and Zeocriton, a very dense variety. The F_2 gave somewhat similar segregation as in preceding crosses, but the F_3 lines showed intermediates as well as extremes breeding true. Certain F_3 families were as variable as F_2, others were more variable than the parents, and still others were homozygous. Four possible modes of density were found in which homozygous segregates were obtained, the very dense with means from 2.1 to 2.3, the dense with means ranging from 2.8 to 3.2, the lax with means ranging from 3.4 to 3.7, and the very lax with means ranging from 4.2 to 4.3. If a large number of types could have been tested, it seems very reasonable to conclude that homozygous forms with an almost continuous range in average length of internode from the very dense to the very lax could have been obtained. Several main density factors are here involved together with minor factors.

The Barley Awn in Relation to Yield.[1]—The long rough awn of barley makes the crop very disagreeable to handle. Hooded varieties have been frequently tried out but have not been extensively grown because they do not yield as well as

[1] See HARLAN and ANTHONY (1920).

standard awned strains. Likewise, many hooded hybrids have been produced but none has proved satisfactory. The facts lead to the conclusion that "the awn is an organ that is functional under most conditions, and especially in those sections where humid weather prevails, at ripening time." A study of the effect of the removal of the awns on the development of the seeds of the spike showed that spikes with awns removed (clipped spikes) produce a lower weight of dry matter at maturity than normal spikes. As the seeds develop as rapidly for several days, after the awn is removed, in clipped spikes as in unclipped, the difference in development at maturity is not due to the shock of removing the awns. About one week after flowering, the deposit of dry matter in the normal spikes begins to exceed that in the clipped spikes. This is stated to be at the time rapid starch infiltration begins. Normal spikes at maturity, near Aberdeen, Idaho, have a content of more than 30 per cent. of ash in the awns. The rachises of the clipped spikes at maturity contained about 25 per cent. more ash than those of normal spikes, which probably accounts for the greater tendency of clipped spikes to break.

These facts show that under humid conditions there is a physiological reason why awned varieties yield higher than hooded or awnless varieties. They are given as an illustration of the value to the plant breeder of a knowledge of the physiological functions of the various organs of plants.

Two methods of attack are outlined for the barley breeder: (1) The use of varieties which normally have a low percentage of ash in the rachis might make possible the production of non-shattering hooded and awnless sorts. (2) The production of smooth-awned varieties, which in a large measure, would overcome the objection to the barley awn.

The production of high-yielding smooth-awned varieties is not a difficult task, as has been learned by coöperative studies carried on at the Minnesota Station. As smooth awn is a recessive character, all that is necessary is to cross high-yielding toothed varieties with smooth-awned sorts, and then select smooth-awned plants in F_2. These will breed true for the smooth-awned character. Numerous plants should be selected, as some will prove more valuable than others for economic characters such as yield, non-shattering habit, and stiffness of straw.

SOME RYE STUDIES

Wild rye, *Secale montanum*, differs from cultivated rye in its perennial habit. Tschermak (1914) finds that wild and cultivated forms may be easily crossed, which indicates rather close relationship.

Rye (see page 40) differs from the other small grains in that it is cross-pollinated. Sterility is often obtained when self-fertilization is attempted. For this reason it is not easy to produce homozygous strains and therefore few inheritance studies have been made.

Xenia in rye was first discovered by Giltay in 1893. It was later corroborated by Von Rümker and others (1913, 1914). By continuous selection, strains have been produced which are pure for color differences. According to Von Rümker, selection for seven or eight years was necessary in order to isolate strains which were homozygous for color of seed. He found the color to be located in the aleurone layer just inside the epidermis. There are numerous colors of rye which are roughly analogous to the aleurone colors of corn. The inheritance of these colors has not as yet been intensively studied. Von Rümker has isolated pure races for greenish blue, deep brown, and yellow seed. There are also deep blue, light brown, and striped seed besides other color variations. In crosses between green- and yellow-seeded strains Von Rümker found green dominant and obtained a ratio of 3 green to 1 yellow in F_2.

There are both spring and winter varieties of rye. The spring habit appears to be a dominant character, for Tschermak (1906) obtained a ratio in F_2 of 3 spring forms to 1 winter form.

Wheat-rye Hybrids.—Numerous investigators (Backhouse, 1916–1917; Leighty, 1915, 1916; Jesenko, 1911, 1913; McFadden, 1917) have reported crosses between wheat and rye. In all reported successful crosses, wheat has been used as the female parent. Rye is very winter hardy and as winter wheat is much less hardy it is only natural to try to improve winter wheat by a rye-wheat cross. As a rule the F_1 cross is self-sterile, although back crosses with the parents have sometimes been successful. Love and Craig (1919 a) have described a successful wheat-rye cross, using Dawson's Golden Chaff as the wheat parent. Studies have been continued through F_4 and F_5 and a number of plants have been obtained which exhibit little or no sterility.

These plants are wheat-like in spike and seed characters, yet they resemble rye in some other characters. They are now being tested for winter hardiness.



FIG. 25.—Spikes from four F_4 plants of a wheat-rye cross. Spike No. 39 is much like rye in regard to the awn development and ciliated glumes. Other heads resemble wheat more than rye. (*After Love.*)

BUCKWHEAT[1]

Buckwheat belongs to the buckwheat family (*Polygonaceæ*). The original home of this plant was probably Asia, whence it was introduced into Europe through Tartary and Russia in the middle ages. The generic name of buckwheat, *Fagopyrum*, comes from the Latin, *fagus*, beech, and the Greek, *puros*, wheat, based on the fact that the seed of buckwheat resembles the beechnut. The three species of economic importance are *F. emarginatum*, *F. tataricum*, and *F. esculentum*. The forms commonly grown in the United States belong to the last-named species. Classification is based on such characters as size, color, and shape of seed; color of growing stem; average height of plant; shape of leaf; and flower characters. The flowers of buckwheat are dimorphic, *i.e.*, some have long stamens and short styles, others just the reverse. Only one kind of flower is produced on the

[1] CARLETON, 1916.

same plant. According to Carleton, seeds of either form of plant produce both kinds, and the ratio is not influenced by soil quality. Dimorphism facilitates cross-pollination.

Breeding Buckwheat.—Little attention has been given to the improvement of buckwheat by breeding. It shows considerable variation, and undoubtedly strains could be isolated that would surpass present commercial varieties. Selections for yield are being made in the United States. In Russia some work is under way to produce strains or varieties with four-faced seeds. These are supposed to be more resistant to early spring frosts.

RICE

Rice is thought by Carleton (1916) to have "originated somewhere in the region from China to India inclusive." It has not been recorded with other cereals that were grown in Egypt in ancient times. Little study has been made regarding classification and genetic relationship of the wild and cultivated species.

Cultivated races are classified into glutinous and non-glutinous groups. Other characters of importance in varietal classification are size, shape, and color of seed; color of glumes and leaf sheath; awned or awnless glumes; and length of glumes, whether long or short. A short summary of inheritance of some individual characters is of interest. (See Table XVIII.)

Inheritance of Characters.—The endosperm of rice is glutinous or starchy. The glutinous group is not grown in the United States or generally in Europe as a commercial crop. On cooking, it runs together into a pasty mass while the seeds of common rice keep their shape when properly cooked. The starch of ordinary rice is replaced by a sort of dextrine in the glutinous varieties. Apparently one Mendelian factor difference separates these groups. The color of the seed is also an endosperm character. Blue is dominant over red and red over white.

The inheritance of plant characters may be explained by the usual Mendelian method. The ratios given show that color inheritance may be explained by one or more factors. Ikeno (1918) studied the inheritance of a number of size characters. In some cases dominance was obtained in F_1. In other characters the F_1 was intermediate. Complex segregation occurred in F_2 but with no definite ratios. Multiple factors were used to explain the results.

TABLE XVIII.—SUMMARY OF INHERITANCE OF CHARACTERS OF RICE

Contrasted characters	F_1	F_2	Authority
		ENDOSPERM CHARACTERS OF RICE	
Character of endosperm	Starchy	Segregation, 3 starchy to 1 glutinous	Ikeno, 1914; Hoshino, 1915.
Red *vs.* white seed	Red	Segregation, 3 red to 1 white	Thompstone, 1915 and Ikeno, 1918
Red *vs.* white seed	Red	Segregation, 9 red to 7 gray, brown and white	Parnell et al, 1917; Ikeno, 1914
		PLANT CHARACTERS	
Red *vs.* colorless awn	Red	3 to 1 ratios	Ikeno, 1918
Palea brown *vs.* colorless	Palea brown		
Palea colorless *vs.* yellow	Palea colorless		
Stigma purple *vs.* colorless	Stigma purple		
Grains not readily falling *vs.* falling	Grains not readily falling		
Susceptibility to disease caused by *Leptosphæria Cattanei vs.* immunity	Susceptibility		
White *vs.* red glume	White	3 white to 1 red	Thompstone, 1915
Long *vs.* short glume	Short	3 short to 1 long	Parnell et al, 1917
Awned *vs.* awnless glume	Awned		Hoshino, 1915
Black *vs.* reddish brown awn	Black		Hoshino, 1915
Green *vs.* golden color of inner glume	Green or intermediate	3 green to 1 golden or 1 green, 2 intermediate, 1 golden	Parnell et al, 1917
Red *vs.* green leaf sheath	Red	9 red to 7 green	Hector, 1916
		QUANTITATIVE CHARACTERS	
High *vs.* low stature	F_1 almost perfectly dominant	Complex segregation (multiple factors)	Ikeno, 1918
Long *vs.* short panicle			
Thick *vs.* thin stem			
Amount of tillering	F_1 intermediate	Complex segregation (multiple factors)	Ikeno, 1918
Time of appearance of first panicle			
Compact *vs.* loose grain arrangement			
Broad *vs.* narrow leaf			
Time of flowering	Intermediate	Segregation	Hoshino, 1915
Quality of grain and yield		Improvement in later years in quality and yield	Kock, 1917

Time of culm formation was carefully studied by Hoshino (1915), who crossed an early with a late variety. The parents averaged 83.8 and 113.2 days, respectively, from time of planting to jointing, the parental average being 98.5 days, while the F_1 gave an average of 94 days from planting to jointing. The F_2 generation equalled the combined range of the parents. Some forms bred true to the parental types in F_3. One form which segregated in F_3 was much less variable than the F_2. This line could be explained by the presence of a single heterozygous factor for time of shooting. The author suggests that three multiple factors will explain the results.

Kock (1917) crossed Karang Serang, an early maturing good quality rice, with Skrivimankotti, a variety of high yielding ability. Results were not easily explained on a factor basis. After seven years some hybrids showed considerable uniformity. Improvements in quality and quantity of yield were obtained as shown by a comparison of the parents and the better of these hybrid lines.

These facts show that correct methods of breeding rice are similar to those of the other small grains.

CHAPTER VIII

METHODS OF BREEDING SMALL GRAINS

The progeny test is now recognized as the best means of determining the comparative productivity of varieties and strains. Vilmorin's isolation principle was first used in the United States in 1897 by Hopkins, of Illinois, for corn breeding, and in 1890 by Hays, of Minnesota, for small grains. Studies in field-plot technic and in crop genetics have led to standard methods of breeding self-fertilized crops.

One of the important steps for the breeder is to obtain a broad knowledge of the crop plant with which he is to work. This consists of a knowledge of the home of the plant, its wild and cultivated relatives, the existing varieties and their important economic characters. It is also necessary to learn the needs of the crop for the locality in which the breeder is to work. The importance of this knowledge can not be over-emphasized. After obtaining a fundamental knowledge of the crop, the work in crop improvement naturally falls under three heads: (1) Introduction, (2) Selection, (3) Crossing. Before taking these up, attention will be given to a system for recording plant pedigrees.

Method of Keeping Continuous Records.—There are numerous methods of keeping records and as a rule each investigator will modify some general scheme to fit his own particular needs. It is also recognized that a plan which might prove satisfactory for an experiment station investigator who works only in one particular region might not be at all desirable for a federal worker who has charge of crop investigations over a wide area.

The Minnesota plan has proved quite satisfactory, although it is recognized that other methods of equal simplicity and value have been developed by other workers. It is given only as suggestive of the necessity of accurate records and as one means of attaining that end. When a new introduction is first brought to Minnesota it is given a Minnesota accession number and the history, source, and other data are entered in the number book for that crop. If the new introduction is a pedigreed form from a nearby state and seems promising it is placed at once in the

variety test. If its value is unknown it is handled in the plant-breeding nursery. The three groups, introductions, selections, and crosses, are given nursery class and stock numbers for means of identification. The year of the first test in Minnesota is also carried (except in the case of crosses where the year that the cross was made is used), together with a series number from 1 to as many forms as are handled in the class for the year and crop concerned. The following classes are used with the supposition that the forms were first tested in the nursery in 1920:

Class I–20–1, I–20–2, etc..... Selections.
Class II–20–1, II–20–2, etc..... Crosses.
Class III–20–1, III–20–2, etc..... New Introductions.

Supposing for example 20 new wheat introductions were grown, these would be classed as III–20–1 to III–20–20. All individual plant selections are placed in class I if they are made from commercial varieties or new introductions. The year that they are first placed in the nursery is also carried, as well as the series number. These class and series numbers are not changed as long as the form is continued in the nursery trial.

Crosses are not given a series number until the strain gives evidence that it is homozygous. For the first few years the method of numbering used by the United States Department of Agriculture is followed. Thus a cross made between I–14–1 and I–14–20 is labeled at the time of crossing I–14–1 × I–14–20. The female parent is written first. On growing this cross in F_1 a convenient number or letter is used. Later generations for the letter method would appear as *A* for F_1, *A*–1 for F_2, *A*–1–1 to *A*–1–200 if 200 plant selections were grown in F_3. As soon as a cross is purified, that is, when particular selections appear homozygous, they are placed in the rod-row test and given a series number; thus the cross made in 1918 would be labeled as follows:

First year, Class II–18, *A*
Second year, II–18, *A*–1
Third year, II–18, *A*–1–1 to *A*–1–200

Suppose *A*–1–10 and *A*–1–50 appear homozygous and look promising, they would be placed in the rod-row test and receive series numbers as II–18–1 and II–18–2.

Bank figuring books have been found to be quite satisfactory

for the yearly field notes, a separate book being used for each crop. The following illustrates the method of keeping records for the year 1922.

Name	N.S.N.	1921 Source	Height, in.	Date heading	Other field notes
Turkey × Odessa..	II–18–1	*A*–1–10			

After obtaining yield and taking notes on grain characters, the yearly results are drawn off on 8½ by 11 paper, summarized, and filed for reference and further study. Only general notes are taken, such as date heading, date mature, height in inches, per cent. lodged, degree lodged, per cent. and kind of destructive diseases, botanical characters, grain color, plumpness and quality, weight per bushel, and yield.

New Introductions.—By means of new introductions the breeder is enabled to obtain varieties or strains which have been produced by other breeders, or native varieties from the original home of the crop. There is no value in attempting to produce a variety which is adapted to a particular condition if the qualities desired are to be found in some variety already grown in another locality or country.

The United States Department of Agriculture has a trained corps of workers who are constantly introducing new plant sorts from foreign countries. At the present time the Office of Cereal Investigations of the Bureau of Plant Industry acts as a medium for the introduction of new varieties of small grains. Through coöperation with this office, promising new introductions are being tested in localities to which they seem adapted.

In small grains no conclusion can be drawn from the first-year test of a new introduction obtained from a widely different climate. Often the seed does not give a high percentage of germination or for some other reason the results secured are not even indicative of the value of the introduction. The first year the different introductions may well be grown in short rows. The following year a rod-row of each new introduction may be grown as a part of the regular crop breeding row trials, and yield and other characters determined. Those which are at all promising by this test may then be placed in the regular row trials and handled in the same manner as pure-line strains. After two or three years those introductions which give results of promise will be used as a basis for individual plant selection, providing the introduction was not already a pure-line.

Selection.—The plant-selection method is used for the purpose of isolating the best possible pedigreed strain of a commercial variety. If the variety is of considerable value a large number of individuals (500 to 1,000) may be selected. Often a smaller number is all that the breeder can afford to test. The number chosen will depend on the productive capacity of the commercial variety or new introduction which is used as the basis of selection. Plant selections are grown in short rows the first year, the same number of seeds being placed in each row.

Two general methods have been rather widely adopted for the initial head-selection plot. In either method the same number of seeds is placed in each row. The difference lies in the spacing of the seeds. Some prefer to place the seeds approximately the same distance apart in the row and at sufficient distance (2½ to 3 inches) that the plants can be separately observed. Others scatter the seeds in short rows, placing them so close together that individual plants cannot be differentiated at maturity. The latter method more nearly approximates the rod-row plan and needs less room. In either case the rows are usually a foot apart.

The field, after being carefully harrowed, is raked by hand, if necessary. It is then marked out by the use of a sled marker, from 7 to 12 rows being marked at a time. The rows are opened with a wheel hoe and covered either with it or a rake or a hand drag with numerous iron teeth.

Those selections which by field inspection seem to be of inferior vigor, to have weak straw or other undesirable characters, are eliminated before harvesting. A few others are discarded on the basis of yield, although the experimental error in a yield comparison of this kind is much too large to justify rejection. The following year each selection may be grown, if sufficient seed is available, in three systematically distributed 18-foot rows, 1 foot being removed from each end of every row before harvesting.

According to Love and Craig (1918a), J. B. Norton, of the United States Department of Agriculture, was the first to put the rod-row method into general use. By varying the length of the row and obtaining the yield in grams it is possible to convert yields into bushels per acre by multiplying by a simple conversion factor. If the length of oat rows harvested is 15 ft. and the yield is obtained in grams, the yield per acre in bushels may be obtained by multiplying by 0.2. For wheat and barley,

if the rows harvested are 16 and 20 ft. long, respectively, the conversion factor will be 0.1.

The rod-rows are about twice as far apart as the rows made by a field grain drill. As from one and one-half to two times as much seed is planted per nursery row as under field planting, the rate of seeding per acre does not differ materially in the two methods. These row trials have been shown to give results similar to those from field tests, although the average yield of the crop is not the same (Montgomery, 1913; Love and Craig, 1918a).

As has been previously noted, there are two general methods of work, *i. e.*, the use of single- and three-row plots. Three-row plots in which the central row only is used to secure yield are desirable as they help to control mixtures at planting and harvesting time, overcome competition between nearby varieties and help in obtaining more dependable data on lodging. They require more land and the cost is somewhat greater for planting and cultivating. In sections where soil heterogeneity is very great it is possible that the use of single-row plots and numerous replications may be somewhat better than three-row plots and fewer replications. On land that is well suited for field plot work the use of three-row plots and three replications is advised.

After a strain has been grown for three years it may well be removed from the row-yield trial and either increased if it shows promise or discarded if it appears to be of no value. At Cornell new sorts are introduced to the farmers for trial directly from the rod-rows. In many cases the new sort is finally tried in variety plots planted by the usual field-plot method. This gives an expression of yield under normal methods of planting and favorable field conditions.

Summary of Methods of Selection.—1. Determination of the varieties which possess economic possibilities. These may be commercial varieties or new introductions.

2. Head selection of these promising varieties.

3. Test of head selections in plant-rows. The very undesirable strains are eliminated in the field by inspection. A few may be discarded on the basis of yield or seed characters.

4. Yield determinations of the selections, using three plots of a single row each, systematically replicated, if seed is available.

5. Continuation of the row test. When land is well suited it is believed that four systematically distributed plots of three rows each will give reliable results. Possibly the arrangement

of selections of like nature together, the use of single rows and more replications, may be desirable under certain conditions.

6. Computation of a probable error for the method of test. The use of this probable error as a means of determining significant differences.

7. Increase of the better selections and either a trial by careful farmers or a further test in field variety plots followed by distribution of the better strains. If placed in field variety plots, borders should be removed and each variety tested in replicated plots. Probable errors should be obtained and used as in the row trials.

From five to eight years' time is needed before the new selection is introduced to the farmer.

Crossing.—The improvement of commercial varieties of self fertilized small grains by the head or plant method of selection is a very easy process, although several years are required to do the work. The production of new forms by crossing is not so simple. A standard plan of attack has been developed which is the application of the Mendelian method.

The first step is the initial cross. Promiscuous crossing is not advised, but each cross should be the result of a determination of parents which most nearly approach the ideals in mind. By recombination of characters there is the possibility of obtaining a sort which is more desirable.

The F_1 generation is grown so that each plant has space for individual development. A knowledge of the inheritance of characters allows those plants which are not crosses to be eliminated in F_1. The F_2 generation plots should be as large as can be studied and each plant grown with enough free space that it may be examined. Numerous selections of plants which have desirable field and seed characters should be made. Each of these F_2 plants selected should be grown in an individual progeny plot in F_3 and individual plant notes taken. Selection of desirable plants should be continued in later generations. When plots show apparently uniform progeny of a desirable sort, the strain should be included in the rod-row tests and compared with standard varieties.

Knowledge of the results of continued self-fertilization in generations following a cross, shows the reliability of another method which was first used at Svalöf, Sweden (Babcock and

Clausen, 1918) and is now being tried by other investigators. It consists of growing a bulk plot of the cross for several generations. At the end of from six to ten years, head selections may be made with the knowledge that a large part of these selections will breed true. The adoption of this plan will in a large measure do away with the technic of studying individual plants in a heterozygous population. It is desirable for those workers who would like to use crossing methods but who do not have time for individual plant studies. It is not so rapid as the Mendelian method.

Technic of Harvesting, Thrashing, Etc.—Slight variations in methods are used by different workers. At Cornell rows of like kind are taken to the thrashing shed and hung head down until thrashed. At the Minnesota Station the straw is cut near the base, the bundles tied with the stake, label near the bottom, and the heads wrapped with a cheese-cloth covering. Bundles of the same selection are then tied upright to a stake and later taken to the thrashing shed when needed. The row trials at the substations are harvested by cutting off the heads. These are then put into cloth sacks and shipped to the Central Station.

Several machines which can be cleaned easily have been devised for thrashing. The chief requisites of a machine to be used for experimental purposes are that it be easily cleaned and that so far as possible there be no ledges or ridges upon which seeds may lodge. The alternate thrashing of different nursery crops is a desirable procedure. Each of the plots of one strain of wheat may be thrashed separately in rotation and then a strain of oats may be thrashed in the same way. At the Minnesota Experiment Station winter wheat is thrashed alternately with barley and spring wheat with oats. This plan helps materially to reduce the roguing of accidental mixtures from the plots.

Various machines have been made to assist in individual head and plant thrashing. A machine constructed by H. W. Teeter, of the Department of Plant Breeding at Cornell (Love and Craig, 1918a), is very satisfactory. As no screen or fan is used, all seeds are saved. After thrashing, the seed is passed through a wind blast. This machine is so arranged that mixtures may be avoided.

CHAPTER IX

SOME RESULTS OF SELECTION WITH SELF-FERTILIZED CROPS

In its broadest sense, selection is really at the basis of all animal or plant improvement by breeding. Evidence accumulated by early plant breeders indicated to them that selection of the most desirable plants for seed was highly profitable, irrespective of whether the plants were naturally cross-fertilized or self-fertilized. Darwin believed that the mean type of any population could be changed by a plus or minus selection. It was left for Johannsen (1903) to point out the true significance of selection within a naturally self-fertilized crop.

Before discussing Johannsen's pure-line concept and its relation to the improvement of self-fertilized crops by selection, a brief survey of early work on improvement of naturally self-fertilized cereals is desirable.

EARLY INVESTIGATORS IN SELECTION OF SELF-FERTILIZED CEREALS

John Le Couteur and Patrick Shirreff were first to use the progeny test in making selections. The former did considerable work with wheat. In the early part of the nineteenth century he grew what he supposed to be a uniform variety. Professor La Gasca, of the University of Madrid, upon inspecting Le Couteur's wheat in the field pointed out no less than 23 distinct forms. This observation led the latter to make a collection of 150 varieties. Le Couteur simply took it for granted that the progeny of any one individual would breed true. Patrick Shirreff, another breeder of cereals, who lived in the middle of the nineteenth century, worked along somewhat different lines. He searched for the exceptional plant to start a new variety, and discovered seven such varieties.

Frederic F. Hallett also followed rigid selection of individual plants in his wheat breeding. Furthermore, he proceeded on the theory that the selection of the best spike on the plant and the

best seed on the spike would yield correspondingly the best plant. Le Couteur and Shirreff placed all the emphasis on the original plant selection, while Hallett believed he could improve the progeny of an individual plant by further selection. Needless to say, Hallett made no progress after the initial selection. A number of his improved varieties were introduced and widely grown.

Louis Leveque de Vilmorin formulated a breeding principle as a result of a series of experiments performed by himself and his father which was published in monograph form (1852). These early studies were carried on with vegetables and the conclusion was reached that the only way to determine the breeding value of a plant was to grow and examine its progeny. Much study was made by the younger Vilmorin with the sugar beet. This is not a self-fertilized plant, but the principles learned have a direct bearing on selection with self-fertilized crops. In the first few years the problem of determining the sugar content of mother beets without injury to the roots received particular attention. Weighing a small ingot of silver in the juice extracted from a small piece of root was found to be an accurate method of determining density and thus sugar content. Roots of similar sugar content were then used as mother plants and their breeding nature determined. Some gave progeny with high sugar content without pronounced variability; other mother plants gave variable progeny some of which were high in sugar content and others much lower, while some mother beets produced progeny of such inferior sugar content that all were immediately discarded. Later the sugar content was determined by means of polarized light (Babcock and Clausen, 1918). As an example of his results may be mentioned a strain of beets which, after three years' selection, gave juice with an average density of 1.087 while unselected seed grown in the same field gave an average density of only 1.042. Andre Leveque de Vilmorin produced a desirable cultivated form of carrot by three years of selection from wild forms. Louis de Vilmorin also made a collection of wheats and other grains from all parts of the world. After 50 years of selection within isolated lines of wheat, no notable change was observed (Hagedoorn, A. L. and A. C., 1914).

Willet M. Hays, formerly of the Minnesota Experiment Station, was the first in America to adopt the "Vilmorin method" for small grains. In 1891 he introduced what is known as the centgener method of grain breeding (Hays and Boss, 1899).

Briefly, it consisted of growing and harvesting a 100-plant plot from each plant. Selection was continued the following year. The selections of most promise were increased and given extensive trials by farmers. By this method new forms of superior value were discovered.

The pure-line method of breeding self-fertilized crops was independently discovered and later adopted (1891) by the Svalöf experiment station in Sweden. The director of the station, H. Nilsson, was led to its adoption by the accidental discovery that only those plots planted with seed coming from a single plant exhibited uniformity (Newman, 1912). DeVries (1907) says:

"To this accidental circumstance, combined with the exact scientific method of keeping extensive records, the discovery of the cause of the diversity of the cultures was due. For precisely those cultures which were derived from one ear only were found to be pure and uniform, all others offering to the eye a more or less motley assemblage of forms."

The fact that many of the agricultural varieties grown in Sweden at the present time are the result of this method of breeding is sufficient evidence of its success.

In addition to individual plant selection, the older mass selection is sometimes used with self-fertilized crops. Mass selection is the selection of a group of individuals which seem to embody the desired characters. No attempt is made to grow the offspring of the different individuals separately and hence a pure-line study is impossible. In spite of this fact, mass selection sometimes has a place in correct breeding. For example, it may be advantageous to let nature eliminate non-hardy forms of a winter wheat variety before beginning a study of individual plant progenies.

SELECTION WITHIN A PURE LINE

Early in the twentieth century Johannsen (1903, 1913) began his famous experiments with beans and barley which resulted in the discovery of facts which led to the development of the pure-line theory. Johannsen found that selection within a pure line was futile. Table XIX is typical of what he obtained by selection within each of 19 different pure lines of beans.

Since Johannsen announced his pure-line concept, several investigators working with other crops and other characters have verified his conclusions.

TABLE XIX.—SELECTION EFFECT DURING SIX GENERATIONS IN LINE I OF PRINCESS BEANS

Harvest years	Total number of beans	Mean weight of mother beans of the select strains		Difference, $B - A$	Mean weight of progeny seeds of select strains		Difference, $B - A$
		A-minus	*B*-plus		*A*-minus	*B*-plus	
1902	145	60	70	10	63.15±1.02	64.85±0.76	+1.70±1.27
1903	252	55	80	25	75.19±1.01	70.88±0.89	−4.31±1.35
1904	711	50	87	37	54.59±0.44	56.68±0.36	+2.09±0.57
1905	654	43	73	30	63.55±0.56	63.64±0.41	+0.09±0.69
1906	384	46	84	38	74.38±0.81	73.00±0.72	−1.38±1.08
1907	379	56	81	25	69.07±0.79	67.66±0.75	−1.41±1.09

Fruwirth (1917) made selections within a pure line of each of the following: lentil (*Lens esculenta*), vetch (*Vicia sativa*), snap bean (*Phaseolus vulgaris*), field pea (*Pisum arvense*), and white mustard (*Sinapis alba*), but failed to change significantly the mean of the character subjected to selection. In other words, the genotype was not altered. Fruwirth also conducted experiments within pure lines of oats. He selected for number and length of hairs on the lower grain in addition to selecting for percentage of two-grained spikelets per plant. The work was carried on from 1906 to 1915 without effecting permanent alteration in the hereditary complex. Table XX taken from Fruwirth, illustrates a typical case.

TABLE XX.—SELECTION FOR PERCENTAGE OF BRISTLING IN OATS

Year	Minus selection			Plus selection		
	Per cent. of bristling of			Per cent of bristling of		
	Parent	Progeny		Parent	Progeny	
		Mean	S.D.		Mean	S.D.
1907	[1]. . . .	5.11±0.68[2]	1.68±0.48[2]			
1908	2.5	5.47±1.37	4.32±0.97	4.8	4.05±0.88[2]	2.78±0.62[2]
1909	0	4.70±1.03	3.24±0.72	9.2	4.75±0.99	3.12±0.69
1910	0.67	2.94±2.36	11.80±1.66	10.0	8.46±1.61	8.06±1.14
1911	0	0.14±0.07	0.33±0.05	21.9	8.88±1.47	5.50±1.04
1912	0	0.93±0.22	0.85±0.12	18.7	1.02±0.35	1.65±0.25
1913	0	1.20±0.33	1.67±0.24	5.1	3.58±0.98	4.18±0.69
1914	0	0.04±0.09	0.44±0.06	13.0	0.64±0.25	1.25±0.17
1915	0	2.65±0.46	2.32±0.33	5.7	3.14±0.55	2.74±0.39

[1] Practically no bristles.

[2] Mean error.

In the above table mean error is used instead of probable error (mean error $\times$ 0.6745 = probable error). The means, both in the minus and in the plus direction, show no effect of continuous selection.

In 1914 Hutcheson published the results of 13 years of continuous selection in wheat carried on at the Minnesota Station. Here again no significant effects of selection are found. Table XXI presents a comparison of the yields for the first five-year period with those of the last five-year period.

TABLE XXI.—COMPARISON OF AVERAGE YIELD PER PLANT IN GRAMS OF FIRST FIVE-YEAR PERIOD WITH THOSE OF LAST FIVE-YEAR PERIOD IN CONTINUOUS SELECTION OF WHEAT

Variety	First five-year period	Last five-year period
Hedgrow	2.67	2.34
Russian	1.99	2.18
Speltz	2.51	2.40
Kamouska	2.01	1.97
Polish 1	1.54	1.61
Polish 2	1.62	1.31
Average	2.06	1.97

In the tobacco breeding work of the Connecticut Experiment Station (Hayes, 1913b) the inheritance of number of leaves was

TABLE XXII.—NUMBER OF LEAVES OF SUMATRA, 403; BROADLEAF, 401; HAVANA, 402; AND CUBAN, 405

Number	Year grown	Leaves of parent	Progeny			
			Range of variation	Total	Average	C.V.
403	1910	..	24–31	150	28.2±0.08	5.27±0.21
403–1	1911	29	23–31	125	26.5±0.11	6.64±0.28
403–1–2	1912	29	21–32	151	26.2±0.12	8.28±0.32
401	1910	..	17–22	150	19.2±0.05	5.00±0.19
401–1	1911	20	16–22	108	19.1±0.08	6.54±0.30
401–1–1	1912	22	17–23	145	19.9±0.07	6.03±0.24
405	1910	..	16–25	150	19.9±0.08	7.53±0.28
405–1	1911	21	18–23	124	20.6±0.07	5.29±0.23
405–1–1	1912	23	17–25	150	20.9±0.07	6.17±0.24
402	1910	..	17–24	150	19.8±0.07	6.98±0.27
402–1	1911	20	16–25	143	20.3±0.10	8.87±0.35
402–1–1	1912	20	17–22	150	19.4±0.05	4.59±0.18

studied. The parental forms were grown with the hybrids for comparison. Although tobacco is naturally self-fertilized, the plants were bagged to insure self-fertilization. The behavior of the parental forms selected in a plus direction is shown. It is obvious from the data presented that tobacco, like other self-fertilized crops, does not respond to selection within a pure line; at least not to a degree which would encourage the plant breeder to use this method of seeking improvement. (See Table XXII.)

Love and Craig (1918b) recently reported on the effect of selection for height of plant within a pure line of oats. No evidence of selective effect was obtained, as is shown in Table XXIII.

TABLE XXIII.—SELECTION FOR HEIGHT WITHIN A PURE LINE OF OATS

Year	Average height of parents selected, in cm.		Average height of offspring produced, in cm.	
	Tall line	Short line	Tall line	Short line
1913	85.8	58.8	74.2	75.7
1914	86.9	60.4	82.6	82.9
1915	94.9	67.8	89.4	88.8
1916	97.1	74.9	95.9	94.5
Average..	91.2	65.5	85.5	85.5

An average difference of 25.7 cm. in height of plant between the parent forms chosen, failed to change the genotype.

One of the old mooted questions among investigators of field crops was the relation between the weight of seed planted and the resultant yield. Earlier workers adhered to the belief that the selection of large seed would give increased yield. In a pure line of a self-fertilized crop, heavier seeds possess larger endosperms and consequently contain more stored food material for the young plantlet than the smaller seeds. It seems that it would be possible to have the environment during the germination period such that the larger seeds would have an advantage over the smaller ones. The important fact to bear in mind, however, is that all seeds of the same pure line have the same inheritance.

Some work has been done (Arny and Garber, 1918) on the relation between size of seed planted and resultant yield in Marquis wheat. The seeds were individually spaced 4 in. apart. The relation between the weight of the seed in milligrams, and the resultant yield in decigrams was expressed by means of a

correlation coefficient. The coefficients for the years 1914, 1915, 1916, and 1917 were 0.143 ± 0.038, 0.088 ± 0.028, 0.445 ± 0.020, and 0.478 ± 0.024, respectively. In this investigation each plant was given the same space for individual development. The results show that under these conditions relatively large amounts of stored plant food in the germinating seed may or may not give the resultant plants an advantage, depending on environmental influences other than the amount of endosperm.

Several investigators have attacked this problem from a practical viewpoint. Seeds were separated into light, medium, and heavy by means of a fanning-mill. The productivity of the plants coming from the various classes of seed was compared under field conditions. Some investigators procured a slightly greater yield from plants produced by heavy seed than from those coming from light seed. Others obtained no such difference. Plants from medium or ungraded seed in almost all cases proved as productive as those from heavy seed. The work carried on at the Ohio Station may be taken as a typical example of these investigations.

Table XXIV presents the average results (Williams and Welton, 1911) of an experiment with weight of seed wheat over a period of seven years. The grades are first, second, and third, representing heavy, medium, and light seed, respectively. Two methods of seeding were practiced, namely, a uniform rate by weight and a varied seeding to obtain approximately an equal number of plants on equal areas.

TABLE XXIV.—THE RELATION OF WEIGHT OF GRAIN TO YIELD IN WHEAT
Seven-year Average Results

Grade	Seed used, Av. wt. per bu., lb.	Bushels per acre			Crop harvested av. wt. per bu., lb.
		Uniform seeding	Varied seeding	Average of both series	
First	61.6	31.3	31.3	31.3	59.4
Second	59.8	31.4	30.9	31.2	59.0
Third	57.7	31.3	30.7	31.0	59.0

In the case of oats (Williams and Welton, 1913) a greater difference was obtained between light and heavy seed, but the unscreened seed yielded only a little less than the large seed. Table XXV presents the average data of a four-year period.

TABLE XXV.—THE RELATION OF WEIGHT OF GRAIN TO YIELD IN OATS
Four-Year Average Results

Grade	Seed used		Bushels per acre			Crop harvested, av. wt. per bu., lb.
	Av. wt. per bu., lb.	No. per ounce	Uniform seeding	Varied seeding	Average of both series	
Light.....	27.5	1,052	59.0	59.0	59.0	28.6
Heavy.....	30.7	1,684	58.0	55.3	56.7	28.4
Unscreened...	27.3	1,286	58.4	58.0	58.2	27.8

A current popular belief is that plants from large or heavy seeds yield more than plants from light or small seeds. The data collected by various investigators do not substantiate this view. As a matter of fact, from a practical viewpoint it would be difficult to demonstrate any increase in yield as the result of the use of a fanning mill. The fanning mill, however, is very useful in removing weed seeds or diseased light grains.

SELECTION FOR THE PURPOSE OF ISOLATING PURE LINES

The determination of the better selections requires at least five years. Accordingly, there have been consistent attempts to find some character or characters which were so closely associated with yield or other economic qualities that they were of actual selection value. If such could be found it would be possible to use them as checks on the yield results. Manifestly they would be of especial value in the early period of head selection, for the results from short rows planted from individual heads are not very accurate indications by which to discard selections.

In this connection DeVries (1907) states that "correlation between botanical marks and breeding qualities are to be considered as reliable guides in the work of selection." As an illustration of such correlations, the belief that there is an association between two-grained spikelets of oats and yield may be mentioned. Some of the early data collected at Svalöf indicated that such was the case. After fifteen years further study, five or six of the best yielding oat varieties were examined. Some were three-grained types and others were two-grained types. Newman (1912) in summarizing these results concludes that "there seems, therefore, to be no definite relationship between the yield of a given strain and the number of kernels per spikelet by which it is characterized." The relationship between other characters was

likewise studied, such as early maturity and high yield; short-haired rachilla and high brewing qualities in barley; weight of 1,000 grains in wheat, oats, and barley and yield; stooling with yield and quality; size of spike or panicle and yield. In some cases there seemed to be a relation between yield or quality and some particular character, but when sufficient numbers were studied no consistent association between any one morphological character and yield was found.

Much investigational study has been made on this subject by others and similar conclusions have been reached. At the Minnesota Station correlations between yield and the following characters in wheat have been sought; stooling, height of plant, size of seed, date heading, and date of maturity. In some seasons the early varieties were the better yielders and in other seasons the later varieties.

Stooling was obtained from plots in which plants had room for individual development, and the correlation of stooling and yield was computed for two years for wheat, oats, and barley. Yield was obtained from the replicated rod-row test. The results showed no association between stooling and yielding ability.

Quite consistent association between weight of 1,000 plump seed and yield of wheat as determined by the rod-row test was obtained as is here shown.

TABLE XXVI.—CORRELATIONS BETWEEN WEIGHT OF 1,000 PLUMP SEED OF *T. vulgare* AND YIELD

Number of selections or varieties in the population	Class and year	Correlation coefficient
70	Spring, 1914	0.431 ± 0.066
70	Spring, 1915	0.519 ± 0.059
35	Spring, 1917	0.580 ± 0.076
63	Spring, 1918	0.109 ± 0.084
54	Winter, 1916	0.356 ± 0.080
83	Winter, 1917	0.436 ± 0.060

Fairly consistent results of this nature would seem to show that weight of seed was associated with high yield in wheat. Montgomery (1912) isolated more than a thousand pure lines of Turkey winter wheat at the Nebraska Station and found both large- and small-seeded strains among the higher yielders. Similar results have been obtained at Svalöf.

A study of the correlation between lodging and morphological

characters of the stems of cereals has been carried out at the Minnesota Station (Garber and Olson, 1919). Number of fibro-vascular bundles, area of sclerenchyma cells in the cortex and bundle and other characters were studied in relation to lodging. Stiffness and thickness of wall of the sclerenchyma seemed to be associated in oats but no such relation was found in wheat and barley. No other instance of a close association between any one of the characters studied and lodging was obtained.

Some correlations are of value in selection or in obtaining accurate data. Thus, if one desires to classify a number of selections according to comparative maturity, reliable results may often be obtained by taking such notes as date of awn emergence in barley and date of heading in wheat and oats. In years favorable for normal development, a high correlation between date of heading and maturity has been obtained. In unfavorable years, date of heading is a more reliable indication of the inherited differences between strains in relation to their normal period of maturity than a note taken at maturity.

In general, it seems safe to conclude that no one character is closely enough associated with yield to be of selection value in picking out the highest yielding strain. It is possible, however, in many crops to weed out the very undesirable plants by inspection. The yield test must then be used to determine the better pure lines. This seems reasonable when we realize that yield is the final result of many growth characters. A strain which excels in all characters, such as stooling, disease resistance, size of seed, size of head, fertility, etc., naturally will be a high yielder. As so many characters—of which the above are only a few of the more easily seen—are essential to high yield, no single botanical character is of great selection value. This has led to the present method which is summarized as follows by Newman (1912):

> "Thus instead of basing the isolation of superior individuals purely upon botanical or morphological characters as was formerly the case, the principle has become to select a large number of individuals without special regard to such characters."

The value of these individuals is determined by the study of yield continued over several years.

Numerous experiments have proved the value of this method. In this connection it is of interest to point out progress that has already been made with self-fertilized crops.

WHEAT SELECTIONS

A new winter wheat, Kanred (Jardine, 1917), discovered at the Kansas Experiment Station as a result of testing out 554 head selections made from Crimean (No. 1,435 of the Office of Cereal Investigations, United States Department of Agriculture) is a rather striking example of what may be accomplished by this method of work. As an average of six years' tests, Kanred yielded 4.6 and 5.2 bu. more than Turkey and Kharkov respectively. These varieties gave best results under Kansas conditions until Kanred was found.

Table XXVII shows a comparison in yield between commercial varieties and selections made from them (Love and Craig, 1918a) at the Cornell Station.

TABLE XXVII.—THREE-YEAR AVERAGE YIELD PER ACRE OF WINTER WHEAT VARIETIES AND SELECTIONS MADE FROM THEM

Varietal selections	Three-year average yield per acre, bu.	Gain, bu.
Klondyke	28.2	
Klondyke 126–26	30.4	2.2
Klondyke 126–44	31.3	3.1
Fulcaster	26.0	
Fulcaster 123–23	27.9	1.9
Fulcaster 123–32 (beardless)	30.2	4.2
Red Wave	27.7	
Red Wave 128–47	31.1	3.4

Red Rock winter wheat, which is highly satisfactory in Michigan, comes from a red seed picked out of a white wheat (Plymouth Rock) (Spragg and Clark, 1916). Here we have an example of selecting and increasing an individual obviously different from the type in which it occurred. The red seed may have been due to one of several causes, admixture, natural crossing, or a mutation. Whatever the cause, selection immediately isolated a wheat which was different in appearance and which proved valuable. On a percentage basis, the average yield of Plymouth Rock at the Michigan Experiment Station during the period 1912–1915 is 73.4. The yield of Red Rock for the same period is taken as 100.

Besides yield and quality other characters of economic impor-

tance may be improved by selection. The illustration below, taken from Williams (1916), shows clearly what has been accomplished at the Ohio Station in the way of isolating a strain with stiff straw. The three pure lines shown are selections from the commercial variety Fultz.



FIG. 26.—Variation in stiffness of straw in pure line selections of Fultz wheat. (*After C. G. Williams.*)

OAT SELECTIONS

The Maine Experiment Station has made somewhat extensive studies of pure lines in oats (Surface and Zinn, 1916). The yields of commercial varieties were compared with that of their respective pure-line selections. In Table XXVIII are given a part of the data reported in Maine Agricultural Bulletin 250.

The average of the seven pure lines of Banner for the entire period of the test is 81 bu. per acre, while that of the commercial Banner is 79.7 bu. The average difference for the period of the test between commercial Irish Victor and the four pure lines is nearly 6 bu. per acre.

TABLE XXVIII.—YIELDS OF COMMERCIAL VARIETIES AND PURE-LINE SELECTIONS

Variety	Bushels per acre			
	1913	1914	1915	Mean
Banner (commercial)	62.7	94.5	81.8	79.7
Banner, Maine 355 (p.l.)	71.0	105.3	83.6	86.6
Banner, Maine 281 (p.l.)	73.1	97.0	81.2	83.8
Banner, Maine 351 (p.l.)	70.0	98.2	75.5	81.2
Banner, Maine 230 (p.l.)	69.4	93.8	76.8	80.0
Banner, Maine 307 (p.l.)	66.9	95.8	77.0	79.9
Banner, Maine 286 (p.l.)	70.9	87.1	75.7	77.9
Banner, Maine 357 (p.l.)	70.0	83.1	79.1	77.4
Irish Victor (commercial)	67.0	82.4	76.2	75.2
Irish Victor, Maine 340 (p.l.)	74.1	95.8	83.6	84.5
Irish Victor, Maine 337 (p.l.)	58.4	103.9	79.2	80.5
Irish Victor, Maine 336 (p.l.)	75.3	89.2	75.1	79.9
Irish Victor, Maine 346 (p.l.)	71.9	89.5	77.0	79.5

Kiesselbach and Ratcliff (1917) have reported in Bulletin 160 of the Nebraska Experiment Station the yields of numerous pure lines of Kherson together with the yield of the commercial variety for a four-year period.

TABLE XXIX.—YIELD TEST OF KHERSON OAT STRAINS GROWN IN FIELD PLATS. 1913 TO 1916

Strain No.	Yield in bushels per acre				
	1913	1914	1915	1916	Average
Original	44.4	58.9	29.9	83.0	54.1
21	58.0	71.7	32.4	85.4	61.9
23	61.0	67.3	27.7	85.9	60.5
15	51.8	50.4	26.5	77.3	51.5
25	62.1	64.2	30.7	83.9	60.2
6	64.1	63.2	24.4	81.6	58.3
33	58.5	63.7	35.7	86.1	61.0
27	50.8	67.1	31.7	81.9	57.9
38	62.1	64.9	31.9	81.1	60.0
35	33.9	53.0	22.8	76.7	46.6
4	61.0	67.8	30.5	80.3	59.9
5		65.2	33.3	83.3	
19		50.1	21.4	74.8	

As shown by the last column of the table, only two of the thirteen pure lines gave lower average yields than the commercial variety for the four-year period. They are Nos. 15 and 35.

Among oat selections (Anonymous, 1919) which have proved their practical value may be mentioned Iowa 103, Iowa 105, and Iowar, all of which are pure-line selections from Kherson. These selections were made by Burnett at the Iowa experiment station.

SELECTIONS IN OTHER SELF-FERTILIZED CROPS

An exhaustive account of the work that has been done in isolating and testing pure lines of self-fertilized crops would alone make a large volume. In this somewhat brief treatment only a few typical examples are chosen.

The Iron cowpea (Orton, 1911), which is resistant to wilt, is one of the notable examples of what has been accomplished by the introduction of a promising variety. The isolation of this form alone has produced thousands of dollars for the farmer. M. A. C. Robust bean (Spragg, 1919), which is a selection out of the ordinary navy bean, has proved to be very much superior in yield to the commercial variety. At the Svalöf Experiment Station (Newman, 1912), in Sweden, progress has been made in isolating pure lines of barley which possess superior brewing qualities.

These few examples show the value of selection as a means of crop improvement. The effect of selection is to isolate the more desirable types from the commercial variety. After this has been accomplished, crossing may be resorted to as a method of obtaining a variety which combines the desirable characters of several strains.

CHAPTER X

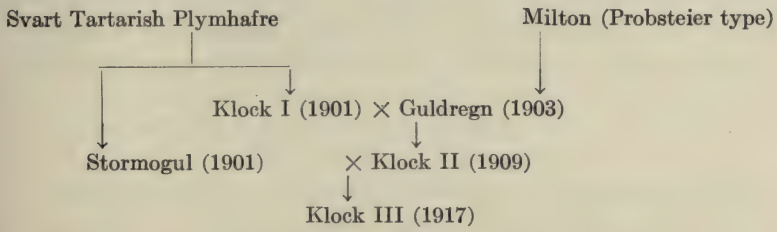
SOME RESULTS OF CROSSING AS A MEANS OF IMPROVING SELF-FERTILIZED CROPS

In the preceding chapters it was shown that the selection and increase of a homozygous individual plant isolated a pure line. No one of these pure lines contains, as a rule, all the characters desired. What usually happens is that one pure line excels in one character, while another is superior with regard to some other character. The only way in which the desirable characters belonging to different strains can be combined is by crossing and then selecting the desired segregate.

To attain success in this field, it is important to use as parents those forms which most nearly approach the combination of characters desired. The old idea of indiscriminate crossing in order to procure superior economic characters, such as yield, has been largely abandoned, which is reasonable from our knowledge of what selection accomplishes and of Mendel's law of inheritance in crosses. Love (1914) compared the yield of oat selections with hybrids which were the result of more or less indiscriminate crosses made by J. B. Norton. The average yield of the hybrids was but little higher than the average yield of the selections. It is probable that the comparison would have shown a greater difference if the parents had been chosen on the basis of their performance records. Two forms may be crossed because each possesses to the greatest degree the character sought, with the hope of obtaining transgressive segregation; or a cross may be made to combine different characters.

The Improvement of Black Oats at Svalöf.—Nilsson-Ehle (1917) has reported experiments carried on from 1901 to 1917 for the purpose of improving the black oats grown in Sweden. The native oats formerly grown had weak straw and lodged badly. Black Tartarian oats was introduced to overcome this difficulty. Little by little this form mixed with the native oats and probably naturally crossed to some extent. The resultant complex (Svart Tartarish Plymhafre) was especially suitable for selection and the

isolation of desirable forms. This was done at the Svalöf Station. The selections, Klock I and Stormogul, maturing early and late respectively, were obtained. Both possess stiff straw and Stormogul has good yielding ability. The improvement of the latter character was sought by crossing with higher yielding light colored forms. The following diagram indicates the method followed. The varieties and strains were purified before the crosses were made.



Klock II is the result of crossing a good-yielding black oat of stiff straw (Klock I) with a high-yielding yellow oat (Guldregn). The offspring has the stiff straw of Klock I and the high-yielding ability of Guldregn. One selection in the cross of Klock II with Stormogul gave a strain, Klock III, which has the early maturity of Klock II, a somewhat higher yielding ability than Stormogul, as well as non-lodging ability, which last character both parents possessed. In Table XXX the yields of three of the strains are shown.

TABLE XXX.—RESULTS OF COMPARATIVE YIELD TRIALS OF THE VARIETIES KLOCK II, STORMOGUL, AND A SEGREGATE KLOCK III OF A CROSS BETWEEN STORMOGUL × KLOCK II AS OBTAINED AT SVALÖF FROM 1912 TO 1916

Grain	Yield per hectare						Relative index Klock II = 100
	1912, kg.	1913, kg.	1914, kg.	1915, kg.	1916, kg.	Average, kg.	
Klock III.....	3,780	4,170	2,560	3,010	4,580	3,620	109.9
Stormogul.....	3,860	4,160	2,700	3,030	4,160	3,582	108.7
Klock II.....	3,730	3,870	2,360	2,280	4,230	3,284	100.0
Straw							
Klock III.....	5,060	4,530	2,470	3,825	7,850	4,747	100.3
Stormogul	5,810	5,330	2,850	4,550	7,630	5,234	110.6
Klock II.....	5,260	4,470	2,310	4,300	7,330	4,734	100.0

A Wheat Cross Made at Svalöf.—The highest yielding winter wheat grown at the Svalöf Station, reported by Newman (1912), was a cross, Extra Squarehead II, No. 0290. This wheat is one of the offspring of Old Extra Squarehead × Grenadier II. It combines the winter-hardiness and rust resistance of the former with the stiff straw and high yield of the latter. As an average of four years' trial at Svalöf and Alnarp, this wheat has yielded 18 per cent. more than Old Extra Squarehead and 8 per cent. more than Grenadier II, which was next. No variety of winter wheat has proved so generally popular among the farmers of southern Sweden as Extra Squarehead II. It may be of interest to point out that preceding the cross, hundreds of selections out of Grenadier II were examined in search of a pure line with the combination of rust resistance and high yield.

Wheat Breeding at University Farm, Cambridge, England.—Most of the wheat varieties grown in England are very susceptible to yellow rust (*Puccinia glumarum*). Biffen (1917) set himself the task of breeding a high-yielding, resistant form. He crossed American Club, which is very resistant to this parasite, with several susceptible varieties in order to study the mode of inheritance and develop a standard technic of operations. In all crosses the F_2 generations showed monohybrid segregation with resistance behaving as the recessive. The resistant individuals were rather clear-cut, although they sometimes exhibited uredinia. The susceptible plants showed a wide range of variation. No recognizable morphological character has been found correlated with resistance.

The constancy of resistance in wheats of hybrid origin has also been studied by Biffen. For the purpose he used a resistant strain produced from a cross between American Club, a resistant variety, and Michigan Bronze, which is one of the forms most susceptible to yellow rust. During eight years of observation the hybrid variety proved just as resistant as the American Club.

A resistant variety of Russian origin, found among some Gurka wheats, which was not adapted to local conditions, was crossed with Square Head's Master, the variety most commonly grown in England. Among the resistant offspring is one that gives considerable promise. Comparative trials of this wheat (Little Joss) over a period of seven years show it to yield about 4 bu. per acre more than the best of the English and French wheats. The explanation for this would seem to be that Little Joss in-

herited the yielding capacity of Square Head's Master as well as the resistance of the Russian wheat parent.

Farrer's Wheat Breeding in Australia.—Probably no one has made more wheat crosses that have proved valuable than William Farrer of Australia (Sutton, 1910). Most of his work was done without the application of a knowledge of the Mendelian principles. He, however, made crosses for definite purposes and in reality followed the Mendelian mode of work without recognizing the law involved. Farrer strongly featured composite crossing, *i.e.*, the crossing of parents which were themselves of hybrid origin. Federation, a variety very popular in southern Australia, was produced in this manner. As a typical example of Farrer's method, the history of Federation will be given somewhat in detail.

This variety was the outcome of a deliberate attempt to produce a wheat especially suited to gathering with a stripper, a harvester used in Australia. Federation is early maturing, stiff-strawed, erect, and of somewhat short growth. Despite its rather unattractive appearance, it is one of the highest yielding wheats for the section in which it is grown. The upright habit makes it easy to harvest. Furthermore, the grains are held tight enough to prevent shattering but not tight enough to interfere with the operation of the stripper. Federation resulted from a cross between the varieties Purple Straw and Yandilla. The parentage is indicated in the following diagrammatic scheme:

Improved Fife × Etawah

Purple Straw × Yandilla

Federation

The history of the origin of Bunyip, another Farrer production, is indicated as follows:

Improved Fife × Purple Straw — Blount's Lambrigg × Hornblende

↓ — ↓

An unnamed cross-bred × King's Jubilee

Rymer × Maffra

Bunyip

Among other varieties produced by crossing which are of economic importance may be mentioned Comback, Cedar, Firbank, Bobs, Florence and Cleveland.

Farrer's method of breeding seems to have been based on inducing maximum variation through composite crossing and then subjecting the progeny to selection. He was a keen observer and possessed ability to pick out forms which proved of economic value. This emphasizes the need of a knowledge of the characters of a crop with which the breeder is to work, which is as essential as a knowledge of laws of breeding.



FIG. 27.—A section of the winter wheat plant breeding nursery in the spring of 1918. The three rows at the right are Minhardi, a very winter-hardy wheat produced from a cross of Odessa with Turkey. In right center are three rows of Turkey, Minn. 1487.

Marquis Wheat.—If the spring wheat known as Marquis (Saunders, 1912) were the only one of economic importance which had been produced by artificial crossing, the practice would be justified. The early history of this wheat is somewhat obscure. It is one of the descendants of a cross between an early ripening wheat from India, Hard Red Calcutta ♀ and Red Fife ♂. The cross was made by A. P. Saunders, probably at the experimental farm at Agassiz, Canada, in 1892. The crossed seed or its progeny was transferred to the Ottawa Experimental Farm. In 1903 Chas. E. Saunders took charge of the cereal breeding at this place and immediately initiated a series of selections from the

progeny of cross-bred wheats. The progeny from the cross made by A. P. Saunders was found to differ strikingly in gluten content of seeds. The laborious practice of chewing a small sample of each pure line was made the basis of selections. One of the high-gluten selections isolated from this mixture of types was named Marquis. It was first grown as a pure form in 1904 and the bread-making tests made in 1907 fully established its bread-making qualities. In addition to this character it is early ripening, thus often escaping rust, has stiff straw, high yielding ability, distinctive appearance of seed, and remarkably wide adaptations. These qualities have made it popular among the farmers in the spring wheat belt.



FIG. 28.—Minhardi, Minn. 1505. Grown in 1918. This variety is very winter-hardy.

Winter Wheat Breeding at the Minnesota Agricultural Experiment Station.—One of the most urgent needs in order to bring about the successful production of winter wheat in Minnesota is a strain which will withstand the severe winters. This ideal has more or less been the goal of breeding operations from the first. Yield and quality also have been given considerable attention. Before attempting crossing, varieties were obtained from all over the world. Odessa, an awnless, red-chaffed variety of Russian origin, has proved most winter-hardy, although

some of the more recent Turkey selections are nearly as hardy. In the large number of crosses that have been studied since 1902 there is an outstanding fact worthy of emphasis from a plant breeding viewpoint. Of the different crosses made, none proved as winter-hardy as the Odessa-Turkey combination, although numerous crosses between other winter wheats were studied. This shows the necessity of studying carefully prospective parental material to determine what should be used. When Odessa was used it furnished an hereditary complex capable of withstanding severe winters (Hayes and Garber, 1919).



FIG. 29.—Turkey, Minn. 529. Grown in 1918. This variety winter-killed very badly.

At University Farm and at Waseca one of the Odessa-Turkey crosses, Minhardi, (Minnesota No. 1,505) has proved more winter-hardy than the Odessa parent. This cross also possesses very high yielding ability but the quality of seed is somewhat inferior. Its ability to yield is probably inherited from the Turkey, which yielded high in favorable seasons. Minturki (Minnesota No. 1,507) is a bearded wheat obtained from a cross of Odessa with Turkey. It is somewhat less winter-hardy than Minhardi but it excels in quality and yielding ability. Table XXXI presents data on some of the more promising forms of winter wheat for Minnesota conditions.

TABLE XXXI.—AVERAGE YIELDS AND AVERAGE WINTER INJURY OF THE BETTER WINTER WHEATS GROWN AT UNIVERSITY FARM AND AT THE WASECA SUBSTATION

Variety or cross	N.S.N.	Minnesota accession No.	Minnesota No.	University farm			Waseca, 1918	Average winter injury, per cent.
				1916, bu.	1917, bu.	1918, bu.	bu.	
Turkey	I-03-213	829	829	24.7	30.0	7.7	40.1	51
Odessa	I-01-3	558	1,471	32.9	36.1	24.8	30.6	38
Turkey × Odessa	II-02-195	829×558	1,505	37.0	43.1	40.9	35.3	29
Turkey × Odessa	II-02-280	829×642	1,507	38.7	47.5	20.9	32.5	42
Turkey	I-03-68	529	1,487	27.5	39.0	5.3	20.2	73
Turkey	I-03-120	1,488	1,488	33.4	40.9	36.5	36.4	40

The pure-line parentage of the Turkey-Odessa crosses is not known, although the parents are believed in all cases to have originated from a single plant. At the time the crosses were made, in 1902, there was no pedigreed Turkey available with the winter-hardy ability of Minnesota 1488. One of the recent crosses made is between the best Turkey selection, Minnesota 1488, and Minhardi. Both parents are winter-hardy and are good yielders; the Turkey likewise produces good quality seed. This shows what is believed to be the correct procedure in plant breeding.

Breeding Beans Resistant to *Colletotrichum Lindemuthianum*.—Extensive tests of the reaction between physiological strains of anthracnose and host plants were made at the Cornell Station. Four groups of beans were obtained; (1) Resistant to both strains, (2) resistant to strain *A* and susceptible to strain *F*, (3) susceptible to *A* and resistant to *F*, (4) susceptible to both *F* and *A*. Wells' Red Kidney was practically immune to strain *A* and highly resistant to strain *F*, while Michigan Robust carried resistance to the *F* strain only. The latter is a white navy bean of superior yielding ability as was pointed out in the preceding chapter. McRostie (1919) crossed these two varieties to obtain a bean which possessed in addition to the characteristics of Robust, resistance to strain *A* of anthracnose. Segregation occurred for resistance to strain *A* on a simple Mendelian 3:1 ratio with susceptibility recessive. In the second and third generations, a white navy bean homozygous for resistance to both physiological strains of anthracnose was obtained.

An Improved Strain of Tobacco.—Connecticut Havana tobacco introduced among Wisconsin farmers gave satisfactory results as

to quality but the yield was low. Johnson (1919), of the Wisconsin Agricultural Experiment Station, attempted to overcome this objection by breeding. In 1909 a pure-line study revealed the fact that there were no less than three distinct morphological types present in the particular variety, grown at the experiment



FIG. 30.—Tobacco No. 27. A pure line strain with a high leaf number and a low breadth index of leaf. (*After Johnson*, 1919.)

station, which was introduced from Connecticut. Selections No. 26 and No. 27 differed distinctly from the normal or prevailing type. Form 26 carried fewer leaves but of larger size than the normal, while form 27 possessed more leaves which were somewhat smaller in size than the normal. A cross between 26 ♀ and 27 ♂ was made in 1910 with the hope of combining the desirable features of the two forms. The success of the cross is indicated in the following data taken from Johnson.

TABLE XXXII.—SUMMARIZED DATA OF MOST SIGNIFICANT CHARACTERS OF CONNECTICUT HAVANA NO. 38 TOGETHER WITH PARENT AND NORMAL STRAINS. AVERAGE OF EIGHT YEARS

Strain	Leaf No.	Average of top, middle, and bottom leaves		Breadth index of leaf
		Length, in.	Width, in.	
No. 26	14.2	20.0	11.3	56.5
No. 27	18.0	18.0	9.6	53.6
No. 38. = 26 × 27	16.9	19.1	10.6	55.8
No. 33	15.5	18.2	9.8	53.8



FIG. 31.—Tobacco No. 26. A pure line strain with a low leaf number and a high breadth index of leaf. Note the method of insuring self-fertilization by covering the terminal inflorescence with a manila paper bag. (*After Johnson*, 1919.)

No. 33 is a desirable strain of the normal Connecticut Havana type produced by continued selection and inbreeding. Breadth

index is obtained by dividing the average leaf breadth by the average length and multiplying by 100. The table shows that by crossing, a form, No. 38, was obtained which combined somewhat the desirable features of the parents (Nos. 26 and 27) and is superior in both number and size of leaves to the better pure-line obtained by selection (No. 33). As an indication of the commercial reception of this new form, it was estimated that at least 10,000 acres of No. 38 were grown in Wisconsin in 1919 out of a total of about 40,000 acres. Here we have an example of crossing two closely-related forms and obtaining from the resultant progeny a strain of more commercial value than either parent.



FIG. 32.—Tobacco No. 38. This strain was produced by crossing No. 26, which excels in leaf breadth, with No. 27, which is homozygous for high leaf number. This new strain is more desirable than any other pure line form obtained. It is widely grown in Wisconsin. (*After Johnson*, 1919.)

The illustrations bring out more clearly some of the features of the parents and progeny.

Summary.—In this chapter concrete evidence of the value of crossing as a means of producing improved varieties of self-fertilized crops has been presented. Crosses should be made with a definite purpose in view and the parents should be selected on the basis of performance records. Just as a chemist requires a certain knowledge of the elements which he synthesizes into compounds, so also the plant breeder may make crosses much more intelligently if he is thoroughly acquainted with the prospective parental material. Promiscuous crossing as a means of producing improved forms is discouraged.

CHAPTER XI

COWPEAS, SOYBEANS, AND VELVET BEANS

Cowpeas, soybeans, and velvet beans belong to the group of naturally self-fertilized crops. The fundamental principles involved in breeding crops of this group have already been discussed. It suffices here to point out that the method of breeding these three legumes does not differ essentially from that for the group.

COWPEAS (*Vigna sinensis*)

Origin.—A wild plant closely related to the cultivated cowpea grows quite generally over the continent of Africa. The wild form differs from the cultivated in having smaller seeds and in having pod valves which coil in ripening. The two forms may be hybridized with ease. This fact and the fact that wild cowpeas have been found in no other place, are generally accepted as evidence (Piper, 1916) that the cultivated form arose in Africa.

Description and Inheritance.—The cowpea resembles the garden bean in general appearance. Some varieties grow erect while others are vine-like and trail over the ground. The pods are rather long and contain from 6 to 15 seeds each. Flowers are white or nearly white and pale to medium violet purple and are shaped like those of the garden pea. Seed coats vary a great deal in color—some are mottled, others uni-colored. The life period of this plant is too long to permit its growth very far north, and for this reason an earlier maturing cowpea is desirable.

Size and shape of pod and seed have been used to separate the larger groups. No studies of inheritance of these major differential characters have been made.

Color inheritance with particular reference to the seed-coat has been studied by Spillman (1911) and more recently by Harland (1919*a*, *b*, *c*, 1920). Anthocyanin coloration in the stem and leaf stalk is dependent on a single factor difference *X*, dominant to its absence. The inheritance of seed coat pattern involves factors *B* (black), *N* (buff), *M* (Maroon) and *R* (Red).

Factor system for seed coat colors:

Black	*B N M R*
Black	*B N m R*
Black	*B n m R*
Black	*B n M R*
Brown	*b N M R*
Buff	*b N m R*
Maroon	*b n M R*
Red	*b n m R*
New-Era pattern	*E R*
White	Absence of *R*

Purple color of the ripe pod is dependent on one main factor difference *P*. Each of the three factors *B*, *E*, and *P*, produces anthocyanin pigmentation in the young pod, calyx, and peduncle. Whether these three factors, each dominant to its absence, constitute a triple series of multiple allelomorphs or occupy different loci very near together in the same chromosome, has not yet been established.

In crosses between black cowpeas and the variety Black Eye, Spillman found the patterns known as Holstein (pigmented area covering micropylar end and isolated spots of pigment on the non-pigmented area) and Watson Eye (pigmented area around hilum with indistinct margin at micropylar end of seed; micropylar end covered with fine dots of pigment) appearing in the F_2 generation. This indicated the origin of varieties which bear these seed-coat patterns.

The inheritance of flower color in the cowpea, according to Harland, is rather simple. In crosses between dark and pale, also between dark and white, the segregation in the F_2 generation proved to be that of a monohybrid with dark behaving as the dominant. Spillman (1913) found correlations between the production of certain seed-coat colors and the occurrence of anthocyan in the flowers.

Root-knot (*Heterodera radicicola*) and wilt (*Neocosmospora vasinfecta*, var. *tracheiphila*) are the two most serious diseases of cowpeas. The former is due to the attack of a nematode whereas the latter is due to a fungus. The variety known as the Iron cowpea possesses resistance to both of these diseases. According to Orton (1911) this disease resistance is inherited as a dominant character. The F_2 generation is too variable to be satisfactorily explained on a monohybrid basis. However, it behaves in a

Mendelian way and hence is relatively easy to transfer and isolate by crossing and selection.

Some Results of Selection and Crossing.—The characteristics of an ideal cowpea are resistance to nematodes and wilt, upright habit of growth with pods borne high, and high yielding ability. With this ideal in view the United States Department of Agriculture has conducted extensive investigations.

Attention was first called to the Iron cowpea by T. S. Williams of Monetta, S. C. He found it would thrive on "pea-sick" soil where other varieties were a complete failure. On learning of this resistant variety, Orton gave it a thorough trial and found it possessed resistance. Measures were immediately taken to in-



FIG. 33.—Iron cowpea vs. Black and Taylor, showing comparative resistance to the wilt and the root-knot. Iron in center and Black and Taylor at right and left respectively. (*After Orton.*)

crease and disseminate the Iron cowpea generally throughout the southern United States. Because the Iron variety did not produce as large yields of seed and forage as some other varieties such as Unknown, breeding was resorted to for the purpose of producing a high-yielding resistant strain (Webber and Orton, 1902; Orton, 1902).

In addition to disease resistance this variety has a relatively upright, bushy habit of growth but the seed production is low. At first a large number of sprawly forms, such as Red Ripper, Clay, Black, and Unknown were crossed with Iron. None of the segregates from these crosses proved particularly desirable.

Later more attention was given to the selection of parents on the basis of habit of growth, fruitfulness, and position of pods. The necessity of a selection of parents on the basis of desired characters can not be over-emphasized. Whippoorwill and New Era are desirable varieties with respect to the three characters mentioned above.[1] The variety Monetta was the best segregate obtained by Orton from a cross between Whippoorwill and Iron. Brabham, a variety which has consistently shown itself superior to Monetta, is the result of the same cross made by a farmer. Both of these varieties of hybrid origin possess disease resistance and to a certain degree the other desirable agronomic characters. More recently Morse, of the Forage Crop Investigations Office, Bureau of Plant Industry, has crossed Brabham with Groit (a hybrid of Whippoorwill and New Era). Victor, one of the segregates of this cross, will be distributed in the near future. Concerning the merits of this new variety, Piper makes the following statement:

"Victor cowpea is absolutely resistant to nematodes and wilt, is a tall bushy variety, extremely fruitful, and, all in all, it seems conservative to say it is by far the best variety of cowpea ever yet developed."

SOYBEANS (*Soja max*)

Origin.—The soybean is of ancient cultivation. Japan, China, Korea, Manchuria, northern India, and the Islands of Java have grown this plant for centuries both as a human food and as feed for animals. In Japan and Manchuria the cultivated soybean is erect in growth. Its nearest wild relative is a small-stemmed, trailing plant with smaller flowers, pods and seeds. This wild form is found in Japan, Manchuria, and China. The varieties of soybeans found in India are intermediate between the two types just mentioned. According to Piper and Morse (1910) all intergrades between the wild plant and the cultivated erect form may be found, so there is little doubt that all forms belong to one species (*Soja max*).

Classification and Inheritance.—The numerous varieties of soybeans show many different combinations of characters. Varieties differ in habit of growth, some being erect, others more procumbent and several truly vining. Color and shape of seed and pods, color of flowers, color of pubescence of the pod and

[1] The following information was furnished by the courtesy of Dr. C. V. Piper.

time of maturity are characters which have been widely used in varietal and group classifications.

Little work has been done on the inheritance of characters in soybeans. Beans with green cotyledons may have green seed-coats, while beans with yellow cotyledons may have either green or yellow seed-coats.[1] H. Terao (1918) of the Imperial Agricultural Experiment Station, Tokyo, Japan, has discovered that in a cross of green cotyledons, green seed-coats ♀ × yellow cotyledons, yellow seed-coats ♂ — the inheritance of the green seed-coat apparently was matroclinal; likewise the inheritance of the character of the cotyledons. In the reciprocal cross the character of the cotyledons again proved matroclinal in inheritance but the seed-coat character segregated as a monohybrid with green dominant. In explanation of these facts it is assumed that the two kinds of chlorophyll concerned differ in that one remains green (*G*) and the other turns yellow (*Y*). It is further assumed that the inheritance of these conditions in the cotyledons is through the cytoplasm or chromatophores and not through the nucleus. In the case of color of seed-coat a Mendelian factor pair is involved. When *H* is present it prevents the chlorophyll (*Y*) in the seed-coat from changing to yellow. When this factor is absent the small letter *h* is used.

Table XXXIII. taken from Terao illustrates four possible combinations. (*G*) and (*Y*) are transmitted only through the cytoplasm of the egg cell.

TABLE XXXIII.—INHERITANCE OF COTYLEDON AND SEED-COAT COLOR IN SOYBEAN CROSSES

	Crossing No. 1			Crossing No. 2	
Parents	(*G*)*HH* ♀ × (*Y*)*hh* ♂			(*G*)*HH* ♀ × (*Y*)*HH* ♂	
Cotyledons	green		yellow	green	yellow
Seed-coats	green		yellow	green	green
F_1		(*G*)*Hh*		(*G*)*HH*	
Cotyledons		green		green	
Seed-coats		green		green	
F_2	(*G*)*HH*	(*G*)*Hh*	(*G*)*hh*	(*G*)*HH*	
	25 per cent.	50 per cent.	25 per cent.	100 per cent.	
Cotyledons	green	green	green	green	
Seed-coats	green	green	green	green	

[1] Black and brown pigments also appear in the seed-coats of certain varieties. These pigments are entirely independent of the green and yellow colors but they make the green and yellow colors indistinct.

	Crossing No. 3			Crossing No. 4	
Parents	$(Y)hh$ ♀ × $(G)HH$ ♂			$(Y)HH$ ♀ × $(G)HH$ ♂	
Cotyledons	yellow		green	yellow	green
Seed-coats	yellow		green	green	green
F_1	$(Y)Hh$			$(Y)HH$	
Cotyledons	yellow			yellow	
Seed-coats	green			green	
F_2	$(Y)HH$	$(Y)Hh$	$(Y)hh$	$(Y)HH$	
	25 per cent.	50 per cent.	25 per cent.	100 per cent.	
Cotyledons	yellow	yellow	yellow	yellow	
Seed-coats	green	green	yellow	green	

The inheritance of color of pubescence of soybeans is simple. The factor for tawny color is allelomorphic and dominant to the factor for gray Segregation for color of seed and color of flower occurred in natural hybrids noted by Piper and Morse (1910). The number of plants observed was not sufficiently large to determine the factors involved.

Breeding.—Pure-line selections of soybeans have been made on the basis of oil content, yield (both of seed and forage), persistence of leaves, and other economic characters. Varieties like Wisconsin Black retain their leaves green until practically all the pods are ripe. Another character of considerable importance in the soybean is frost resistance. It has been found in trials at the Arlington Experimental Farm near Washington, D.C., that varieties differ appreciably in this character in both early spring and late fall. Most of the late varieties were killed. This would indicate that the hereditary difference between varieties in frost resistance is without doubt in part a matter of the degree of maturity which the plants have reached at the time of frost. Considerable artificial hybridizing has been done by Morse of the United States Department of Agriculture. While soybeans have been grown in the orient since ancient times, their general growth in the United States and Europe is comparatively recent. As a consequence investigation with this crop has not proceeded much beyond the stage of variety testing and strain isolation. Then, too, there are so many varieties of different habits of growth, that it has been possible to find a variety adapted to almost any locality. As the real value of the soybean becomes more generally appreciated, it will undoubtedly receive more attention from the breeding standpoint.

VELVET BEAN (*Stizolobium*)

Origin.—Although little is known of the early history of the velvet bean it is thought that it is a native of India. The Florida velvet bean (*Stizolobium deeringianum*) was introduced into Florida previous to 1875 and has never been grown much farther north because of climatic limitations. Southern Georgia, Alabama, Mississippi, and Louisiana mark the northern limits of this thrifty, vigorous growing legume. Cultivated varieties of related species of *Stizolobium* have been found in the countries surrounding the Indian Ocean. The most important of these is the Lyon bean (*S. niveum*). Hybridization between this form and the Florida velvet bean has produced many different types, some of which resemble other species of *Stizolobium*. From this fact, Piper has suggested that possibly all cultivated forms of *Stizolobium* belong to a single species.

Important Characters and Inheritance.—The Florida velvet bean is an annual of extremely vigorous growth. Its branched, vine-like stems sometimes reach a length of from 30 to 50 ft. The leaves are large and compound, bearing ovate leaflets. The flowers, which are dark purple (white in some species), are borne in long racemes. The most important parts of the plant from a feeding standpoint are the pods, together with their seeds. Mature pods carry from three to five marbled brown and gray seeds. The pods are somewhat constricted between the seeds and are covered with a velvety pubescence. Another important agronomic character is dehiscence of pod. The Lyon, which has pods nearly free from hair, scatters its seed when ripe, the Florida velvet bean does not. Pods of different varieties also differ in the degree of susceptibility to rot when in contact with moist soil. The pods of Yokohama velvet bean, from Japan, decay very easily.

Belling,[1] of the Florida Agricultural Experiment Station, has made a study of the inheritance of some of the characters of the velvet bean. He crossed the Florida velvet bean extensively with Lyon bean and to a lesser extent with Yokohama and China velvet beans. The Florida bean has a pubescence of whitish stiff hairs on its leaf buds and young shoots while the ripe pods are covered with brownish black, woolly, flattened hairs mixed with a few stiff hairs. These hairs average 1 mm. in length.

[1] See Belling (1912*a*, 1913, 1914*a*,*b*, 1915*a*,*b*).

The Lyon bean has a whitish stiff pubescence on its young shoots, leaf and calyx. The hairs on the pods form a fine down and average 0.5 mm. in length. The F_1 was covered with irritating hairs. The hairs on the pods were about 1.5 mm. long. These contain a gummy substance in the hollow points and readily pierce the human skin, causing an irritation lasting several minutes. In F_2 about nine-sixteenths of the plants bore stinging pods (long stiff hairs which pierce the skin). Some were more developed than in F_1. Two factors are necessary for the production of stinging pods. One of these factors, B, is contained by the Lyon bean while C is contained by the Velvet bean. Color of pubescence showed segregation in F_2, giving 13 whitish to 3 black pubescent plants. The dehiscence of pods behaved as a dominant. Most of the pods on the F_1 plants burst open when mature. In the F_2 generation segregation occurred. Long pods crossed with short pods gave approximately a 3:1 ratio in the second generation although minor factors for pod length were discovered. In the inheritance of seed color it has been suggested that three factors are concerned, each of which produces some mottling even when heterozygous and in the absence of the two other factors. Purple color appears in the Florida velvet bean on the under surface of the first pair of simple leaves, on the stems as a mark on the leaf axil, on the wings and standard and on the stems and petioles on the side exposed to the sun; while the Lyon lacks the purple color. Purple color proved dominant in F_1 and a 3:1 ratio was obtained in F_2, only a single factor being involved. The characters, time of flowering, size of flower clusters, and size of plant gave unmistakable evidence of segregation in the second generation. Each of the crosses Florida x Lyon, Lyon x Florida, and Florida x Yokohama produced about 50 per cent. pollen sterility in the F_1 generation. Aborted ovules were found on plants showing pollen sterility. Belling satisfactorily explained the results by postulating two factors, K present in Florida, and L present in Lyon and Yokohama. The presence of either K or L, but not both, gave rise to normal pollen and ovules. Combinations of KL or kl in the gametes resulted in pollen or ovule sterility.

Mutations.—Coe (1918) has attributed the origin of early maturing velvet beans to mutations. C. Chapman and R. W. Miller, both of Georgia, and H. L. Bloŭnt of Alabama, separately discovered early maturing mutants growing in fields planted to

corn and Florida velevt beans. Chapman's selection has been increased and distributed under the names "Georgia" and "Hundred-Day Speckled." This variety requires 120 to 130 days to mature. The "Alabama" variety, which matures in 170 to 180 days, or about two months earlier than the Florida velvet bean, was developed from an early maturing plant observed by Blount.

The discovery of these early varieties has greatly increased the acreage of velvet beans by making it possible to grow them farther north. In 1914 less than 1,000,000 acres were grown, whereas, in 1917, over 5,000,000 acres were given to this crop.

Another mutation[1] which is of unusual interest because of the long viny habit of growth of the velvet bean, is the bush form discovered recently in the Alabama variety. The appearance of the bush type has been found in other normally twining beans such as the common bean, the Lima bean, the hyacinth bean, and the soybean. The above mentioned bush or "bunch" velvet bean was discovered by R. Beasley on his farm near Kite, Ga. He carefully saved the seed of a single plant in 1914 and from the resultant crop grown in 1915 obtained about 50 bu. The United States Department of Agriculture is introducing this variety into various localities of the Southern United States.

For some purposes the bush variety possesses distinct advantages. For instance when grown with corn it has no tendency to twine around the corn stalks and pull them down. It is also better suited for use as a hay crop. In appearance of pods and seeds, ability of pods to resist decay when on the ground, and time required to mature, the mutant is practically identical with the Alabama variety.

Breeding.—Some progress has been made in the improvement of the Florida velvet bean by hybridization and selection at the Florida experiment station. A bean is desired which will give a maximum yield of forage and seed of desirable quality. Plants with bristle-like pubescence or small seeds with thick hulls are undesirable. Dehiscent pods and also those which decay readily when lying on moist soil should be avoided. An earlier-maturing strain has been sought by crossing the Florida velvet bean, which requires about 200 days to mature, with Yokohama, which requires about 120 days. It is of interest to point out that from one cross between late varieties (Florida x Lyon) a segregate was

[1] The following information was furnished by the courtesy of Dr. C. V. Piper.

isolated that matured a month earlier than either parent. This promising strain called Osceola has found considerable favor in the south. Another segregate, a variety called Wakulla, obtained from the same cross, matures in approximately 120 days. This strain has an undesirable character in that it shatters its seed when ripe. The material available furnishes an opportunity to obtain further improvement by crossing and selections.

CHAPTER XII

FLAX AND TOBACCO

FLAX

Flax has been reported to have been grown by the Lake Dwellers of Switzerland as early as 4,000 to 2,000 years B.C. (Chapter I). Although the Egyptians and Hebrews used flax to make clothing in very ancient times, little is known of the origin of our present cultivated varieties.

Species Crosses.—Tammes (1911, 1915, 1916) has made some interesting genetic studies of flax species crosses. Reciprocal crosses were made between cultivated varieties of *Linum usitatissimum* and the wild species *L. perenne, austriacum, narbonnenese, grandiflorum,* and *angustifolium.* No seeds capable of germinating were obtained except in the *angustifolium* cross. This was considered a good cause for believing that *L. angustifolium* has the best right of any of the wild species to be considered the ancestral form of cultivated flax. This wild species differs from the common cultivated varieties in that the seeds and capsules are smaller, the edges of the partition walls of the capsule are hairy, and the capsules open at maturity. In general, crosses between hairy and glabrous races showed dominance of the hairy condition in F_1 and a segregation of 3 hairy to 1 glabrous in F_2. The open type of capsule was imperfectly dominant in F_1, *i.e.*, the capsules did not open as widely as in the open parent. Segregation occurred in F_2. Parental types, *i.e.*, homozygous open and homozygous closed lines, were produced in later generations. Three or four factors were necessary to explain results.

Interrelation of Factors for Flower and Seed-Colors.—Careful studies have been made of the interrelation in inheritance of various flax characters (Tammes 1911, 1914, 1915, 1916). The results were carefully analyzed. Three factors called *A*, *B*, and *C*, were shown to be necessary for the production of dark blue flowers. *B* and *C* together produce light blue flowers, and *A* is an intensification factor which in the presence of *B* and *C* produces dark blue flowers. When *C* is homozygous in the presence of *B*, the veins of the petal are darker than the rest of the petal. The veins are the same color as the rest of the petal when *C* is heterozygous in the presence of *B*. *B* and *A* give the

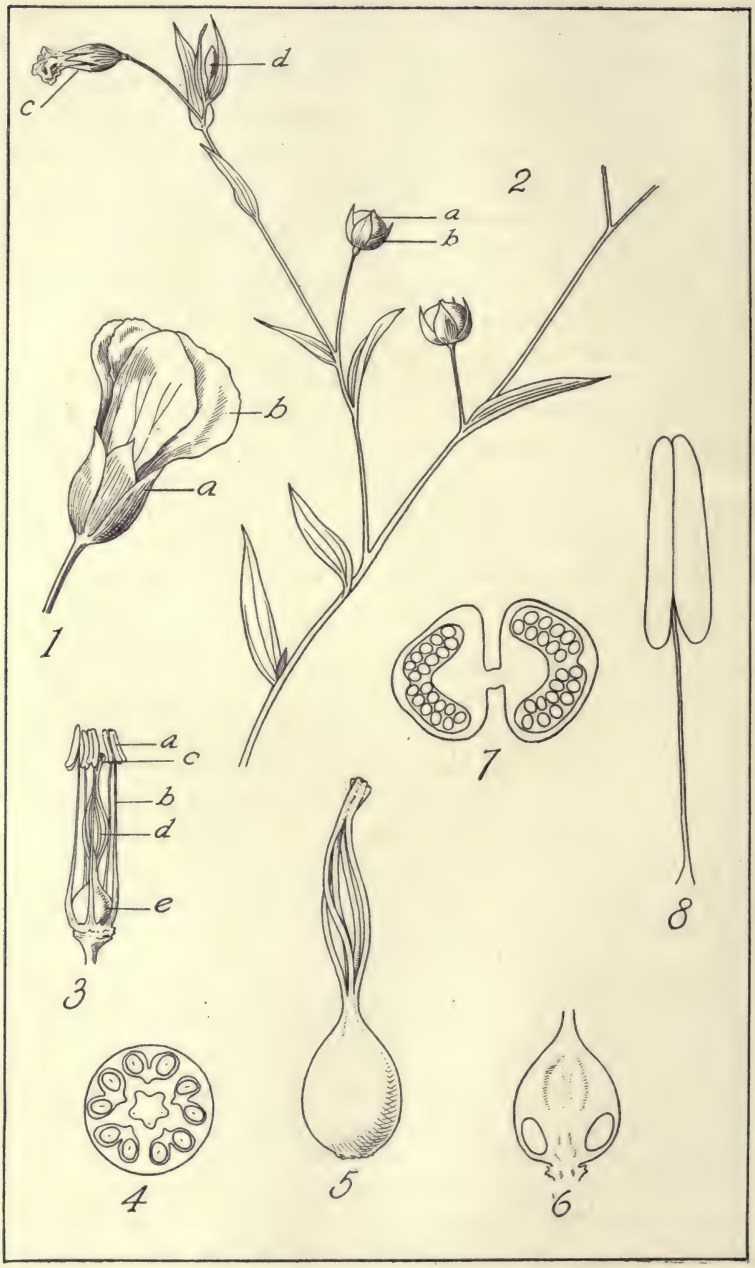


FIG. 34.—Structure of flowers of flax.

TABLE XXXIV.—SECOND AND THIRD GENERATION OF A CROSS BETWEEN A WHITE FLOWERED VARIETY WITH BLUE ANTHERS AND BROWN SEED (*AABB*) AND A CRINKLED WHITE VARIETY WITH YELLOW ANTHERS AND YELLOW SEED (*AACC*)

In this table

d.bl.flr. = dark blue flower
l.bl.flr. = light blue flower
w. = white flower
c.w. = crinkled white flower
br.s. = brown seed
y.s. = yellow seed
bl.st. = blue stamens
y.st. = yellow stamens
with v. = with darker veins than the remainder of the petal
without v. = with veins of the same color as the body of the petal

F_2 expected		F_2 obtained	F_3 expected	F_3 obtained
1 *AABBCC* d.bl.flr. with v., bl.st., br.s.	3	213	Only d.bl.flr. with v., bl.st., br.s.	409 plants in several families.
2 *AABbCC* as above			d.bl.flr. with v., bl.st., br.s. 3 c.w., y.st., y.s. 1	60 21
2 *AABBCc* d.bl.flr. without v., bl.st., br.s.	6	397	d.bl.flr. with v., bl.st., br.s 1 d.bl.flr. without v., bl.st., br.s.. 2 w.flr., bl.st., br.s 1	4 8 2
4 *AABbCc* as above			d.bl.flr. with v., bl.st., br.s 3 d.bl.flr. without v., bl.st., br.s.. 6 w.flr., bl.st., br.s 3 c.w.flr., y.st., y.s 3 w.flr., y.st., y.s 1	31 63 34 23 9
1 *AABBcc* w.flr., bl.st., br.s.	3	203	to breed true.	1,317 plants in several families.
2 *AABbcc* as above			w.flr., bl.st., br.s. 3 w.flr., y.st., y.s 1	1,271 361
1 *AAbbCC* c.w.flr., y.st., y.s.	3	167	to breed true.	395
2 *AAbbCc* c.w.flr., y.st., y.s.			c.w.flr., y.st., y.s 3 w.flr., y.st., y.s 1	obtained such segregation.
1 *AAbbcc* w.flr., y.st., y.s.	1	74	to breed true.	402

DISCRIPTION OF FIG. 34.

1. Single flower—*a*, calyx; *b*, corolla.
2. Branch showing—*a*, seed; *b*, calyx; *c*, flower just after blooming; *d*, bud.
3. Calyx and corolla removed to show sexual organs in position—*a*, anther; *b*, filament; *c*, stigma; *d*, one of 5 divisions of style; *e*, ovary.
4, 6. Cross and longitudinal section of ovary.
5. Ovary, stigma and 5-lobed style.
7. Cross section of anther.
8. Anther.

Size: 1, about $5n$; 2, about n; 3, nearly $4n$; 4–8, greatly enlarged.

same result when heterozygous as when homozygous. *C* alone or with *A* gives wrinkled petals and reduces the number of seeds which set per capsule and induces lower viability of seeds. *B* prevents the above action of *C*. B alone or in the presence of *A* and *C* produces blue anthers and brown seeds. When *B* is absent the seeds and anthers are yellow. Table XXXIV gives the result of one of several similar studies. The tabular presentation shows how carefully these studies were carried out.

Inheritance of Size Characters.—Studies of length of seed were made with crosses of the wild *angustifolium* and cultivated varieties (Tammes) as well as with crosses between cultivated varieties. Seeds were of intermediate size in F_1 and segregation occurred in F_2. The number of individuals grown was not large and the parental forms were not always again obtained. From two to four multiple factors are necessary to explain results.

Length and breadth of petal were also studied. Three forms were used, a small-petalled white-flowered variety with a petal breadth of 3.3 mm., the common varieties with a breadth of 7 mm. and an Egyptian cultivated blue-flowered variety with a mean breadth of petal of 13.4 mm. In the cross between Egyptian blue and common white the factors for color of flower and seed and for size of seed were apparently inherited independently. Breadth of petal ranged from one parent to the other in F_2. Several factors for size of flower were necessary to explain results. The common blue with a petal breadth of 7 mm. was crossed with the small-petalled white with an average breadth of 3.3 mm. In F_2 all blue-flowered segregates agreed in size with the blue parent and all white-flowered segregates had small-sized petals. The cross between Egyptian blue and the small-petalled white gave blue-flowered races with petals of intermediate size in F_1 and segregation for flower color in F_2. The blue-flowered segregates gave a larger average breadth of petal than the white segregates. Three hundred plants of each color were examined.

TABLE XXXV.—CORRELATION BETWEEN COLOR OF COROLLA AND BREADTH OF PETAL IN THE F_2 GENERATIONS OF FLAX CROSSES

	RANGE, MM.	AVERAGE, MM.
300 blue-flowered plants	5.7–16.2	10.8
300 white-flowered plants	2.1–10.4	4.6
Parent Egyptian blue	10.5–16.2	13.4
Parent white-flowered	2.1– 4.2	3.3

These results were explained by supposing that the small-petalled white flax and the common varieties have the same factors for breadth of petal, *C*, one of the color factors, when alone or in the presence of *A* is an inhibition factor for flower size. *B*, when present, prevents the action of *C*.

Wilt Resistance in Flax.—When flax is grown for several years on the same soil, a heavy infection of *Fusarium lini* often results, and complete crop failure may occur. Bolley, as early as 1901, pointed out the true nature of the disease and devised

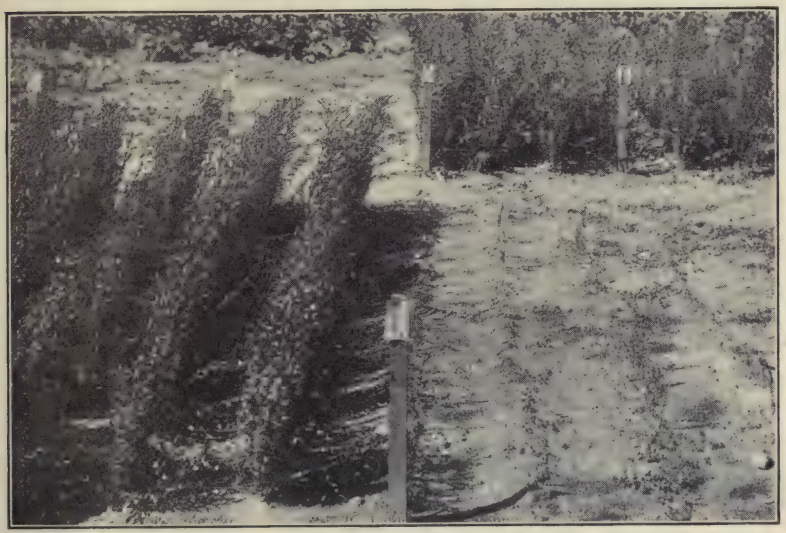


FIG. 35.—Selected and non-selected flax on wilt sick soil. Right foreground, non-selected flax killed by wilt; left foreground, selected flax; left background, non-selected; right background, selected. University Farm, St. Paul, Minn., 1918. (*After Stakman, et al.*, 1919.)

methods for its control. Seed treament and crop rotation were shown to be beneficial as aids in the control of wilt. Seed selection, however, proved the most efficient control measure. In general, Bolley (1903, 1909) found that two or three years' selection under disease conditions were necessary in order to isolate a resistant variety. Both individual and mass selection methods were used. Similar studies carried on at the Minnesota Station (Stakman, *et al*, 1919) have confirmed Bolley's results.

One of the peculiar results of this work is the discovery that resistant varieties lose their resistance after they have been

grown for several years on disease-free soil. Whether this behavior is a gradual decrease in resistance of the host which is roughly proportional to the length of time which the resistant variety has grown on wilt-free soil or a more or less sudden change which appears after two or three years is as yet unknown. The possibility that varietal and strain differences are due to the heterozygous condition must not be overlooked.

As an aid to seed selection in avoiding wilt, early planting is advocated. When planted early, a susceptible variety will often partially escape the serious effects of wilt. Likewise, a resistant variety frequently appears entirely wilt free when planted early, while a later planting may show partial infection.

Tisdale (1916, 1917) has made important contributions to the nature and inheritance of wilt resistance. A high temperature proved to be an especially favorable agent in overcoming resistance. The fungus penetrates the flax plant through the stomata of seedlings, the root hairs, or the young epidermal cells. In the resistant plant, the fungus on entering stimulates cork wall formation of cells adjacent to those attacked, which prevents further invasion. Infection of resistant plants by artificial inoculation of greenhouse or field cultures of *Fusarium lini* did not occur in 43 trials. Check infections of susceptible plants gave 22 successful inoculations out of 47 trials. Tube cultures gave considerable infection of resistant plants although the resistance was marked when these were compared with tube cultures of susceptible strains.

The inheritance of wilt resistance was studied. A great difference in the individuality of plants of the same strain with respect to resistance was shown by their offspring. Wide variation in appearance of F_1 progeny from different crosses of susceptible and resistant plants of the same strains was obtained. Segregation occurred in F_2. A part of the lack of uniformity of results may be explained by varying environmental conditions. Tisdale believes inheritance results can be explained by multiple factors.

Methods of Breeding.—The flax plant is grown for either seed or fiber. Varieties range in height from approximately 1½ to more than 3 ft. Aside from differences in inheritance, the thickness of planting strongly influences the habit of growth. The fiber crop is largely produced in the Old World, while Argentine and the United States are among the leaders in seed

production. Methods of breeding for seed or fiber flax are essentially the same as with the small grains.

TOBACCO

The Genus Nicotiana.—The tobacco genus, *Nicotiana*, has been divided by earlier workers into four sections: Tabacum, Rustica, Petunioides, and Polidiclia (Don, 1838). More recently the latter two sections have been combined (East, 1912*a* and Setchell, 1912). East's conclusions were reached by crossing *N. Bigelovii*, of the Petunioides section with *N. quadrivalvis*, which was formerly placed in Polidiclia section. *N. quadrivalvis* produces four-celled capsules and is a smaller plant than *N. Bigelovii*. As the F_1 hybrid was entirely fertile, there seems no good reason for placing these forms in different sections. The four-celled capsule proved to be a partially dominant character.

From the standpoint of the student of plant genetics the *Nicotiana* genus is especially favorable material. Some of the reasons are:

1. Tobacco may be self-fertilized artificially with ease and the technic of crossing is very simple.

2. Each plant produces a large number of seeds and the seed is viable for many years.

3. There are a large number of varieties which are entirely fertile *inter se*. These furnish especially favorable material for a study of quantitative characters.

4. The different species furnish very favorable material for a study of sterility. Different crosses furnish F_1 generations which differ from each other in sterility. The range extends from species crosses which give no viable seed and from completely sterile F_1 crosses, to entirely fertile ones.

The Tabacum section is represented by numerous varieties of the species *Nicotiana tabacum*. These are natives of the New World. All commercial tobacco grown in the United States belongs to this species.

The Rustica section includes all the yellow-flowering species and varieties. These are of commercial importance in some countries. In India for example, they are successfully grown commercially and for some purposes prove more desirable than the *tabacum* varieties (Howard, *et al*, 1910 *b,c*). Among these rustica forms are three groups; (*a*) one in which the pistil is

longer than the stamen and therefore which must be artificially pollinated by hand or crossed by the aid of insects; (*b*) an intermediate type; and (*c*) forms in which the stamens and pistil are so arranged that self-fertilization is the usual rule.

The Petunioides section contains numerous varieties and species. Many of these are grown as ornamental flowering types.

Parthenogenesis.—Parthenogenesis, meaning the production of viable seed without pollination, was shown by Goodspeed (1915) to occur in *N. tabacum*, variety Cuba. Under normal conditions its occurrence is rare. Wellington (1913) did not find parthenogensis in a considerable series of experiments and with numerous treatments under greenhouse conditions. Several species as well as several commercial varieties of *N. tabacum* were used in this study. Howard (1913) states that parthenogenesis in *N. tabacum* does not occur under normal but may occur under abnormal field conditions, at Pusa, India.

Sterility.—Studies of crosses between *N. tabacum* varieties and *N. sylvestris*, which belongs to the Petunioides section, have been made by Goodspeed and Clausen (1917). The F_1 generation proved to be nearly sterile, although a few apparently normal pollen grains were produced. These could not be caused to germinate in their own stigmatic fluid or in other media. A few normally maturing ovules capable of fertilization were produced by the F_1 plants. If the plants were kept under poor cultural conditions and the flowers pollinated by their respective parents approximately 1 per cent. of the number of seeds normally produced was obtained. If back-crossed with the *sylvestris* parent, practically 10 per cent. of the offspring of the seeds produced are pure *sylvestris*. When crossed with *tabacum*, part of the plants from the seeds produced seem to be of normal tobacco type and are fertile; others resemble *tabacum* but are sterile. The F_1 plants closely resemble the particular variety of *N. tabacum* which is used as one of the parents.

Studies of self-sterility in tobacco crosses have been made by East (1919*a*,*b*,*c*). East and Park (1917, 1918) studied crosses between *N. Forgetiana* and *N. alata* which are self-sterile, and *N. Langsdorffii*, a self-fertile species. *Alata* and *Forgetiana* varieties sometimes produce seed late in the flowering season, although during periods of rapid growth they are entirely self-sterile. The few seeds obtained under reduced cultural conditions

from selfing these self-sterile species are spoken of as cases of pseudo-fertility.

Results of crosses between self sterile and self fertile varieties are given in Table XXXVI:

TABLE XXXVI.—INHERITANCE OF STERILITY IN CROSSES BETWEEN SELF-FERTILE AND SELF STERILE TOBACCO SPECIES

PARENTS	F_1	F_2	
Forgetiana × Langsdorffii	Self-fertile vigorous	144 self-fertile	37 self-sterile
Alata × Langsdorffii	Self-fertile vigorous	162 self-fertile	38 self-sterile

The self-fertile condition proved dominant in F_1 and a ratio of approximately 4 self-fertile to 1 self-sterile plant was obtained in F_2. The self-sterile plants of F_2 proved self-sterile in later generations. East explained these results by a dominant factor, *F*, for fertility and a subsidiary factor, *D*, for pseudo-fertility which exhibits itself only in the presence of the factors for sterility, *ff*. This pseudo-fertility factor produces some fertility under certain conditions, thus tending to lower the number of self-sterile forms.

East has suggested that differences in the rate of pollen germination are largely responsible for the differences in the length of pollen tubes from compatible and incompatible pollinations. When self-sterile plants are self-pollinated the pollen grains germinate but the pollen tubes grow so slowly that abscission of the flower occurs before the pollen tube reaches the ovary.

Color Characters.—Color of corolla has been studied for *Nicotiana* crosses. East (1916*b*) found that in crosses between *N. Langsdorffii* and *N. alata* there was a dominance in F_1 of yellow over white in the color of the corolla. The *Langsdorffii* parent produces blue pollen and the *alata* yellow. Reciprocal crosses gave blue pollen in F_1, although the color was somewhat lighter than in the blue-pollen parent. Results in F_2 showed 342 plants with blue pollen and 100 plants with yellow pollen. Yellow-pollen plants bred true in F_3. Here we have a cross between species which exhibits a monohybrid ratio.

According to Allard (1919*a*) *N. tabacum* exhibits three distinct flower colors—carmine, pink, and white. In crosses between carmine and pink the F_1 was carmine. The F_1 pollinated with the carmine parent gave all carmine colored progeny while the F_1 crossed

with the pink gave carmine and pink in a ratio of 1:1. This indicates that carmine and pink differ in one genetic factor. In a cross of carmine and white the F_1 was all light carmine. In F_2 there were 54 carmine, 95 light carmine, 26 dark pink, 38 light pink, and 65 white. Some of the extracted whites revealed a tinge of color. Crosses of extracted whites with pink gave 32 carmine and 62 pink, showing that extracted whites sometimes carried a carmine factor. The factor relations are not entirely clear.

Quantitative Characters.—Many of the so-called size characters of tobacco are of great commercial importance. For this reason their mode of inheritance is of much interest to the breeder. Extensive studies of inheritance of these size characters have been made. Inheritance of leaf number will be given as an example of a common type of inheritance of size characters in this group. Sumatra, which averages 27 leaves, was crossed with Broadleaf, which gives an average of 19.4 leaves. The results for the parents and F_1 to F_3 generations as obtained at the Connecticut Station are given in Table XXXVII (Hayes, East, and Beinhart, 1913).

TABLE XXXVII.—INHERITANCE OF LEAF NUMBER IN CROSS (403 × 401) SUMATRA × BROADLEAF

Number	Year grown	Generation	Leaves of parent	Range of variation	Total	Mean	C. V.
403 Sumatra	1910	P_1	..	24–31	150	28.2±0.08	5.27±0.21
403–1	1911	P_2	29	23–31	125	26.5±0.11	6.64±0.28
403-1-2	1912	P_3	29	21–32	151	26.2±0.12	8.28±0.32
401 Broadleaf	1910	P_1	..	17–22	150	19.2±0.05	5.00±0.19
401-1	1911	P_2	20	16–22	108	19.1±0.08	6.54±0.30
401-1-1	1912	P_3	22	17–23	145	19.9±0.07	6.03±0.24
403 × 401 = *B*.	1910	F_1	..	19–26	150	23.6±0.07	5.51±0.21
B-1	1911	F_2	25	17–32	2,402	22.7±0.03	8.99±0.11
B-3	1911	F_2	24	17–35	1,632	22.5±0.03	9.51±0.10
B-1-4	1912	F_3	25	16–29	179	22.5±0.12	10.84±0.39
B-1-7	1912	F_3	22	17–28	207	21.5±0.10	10.14±0.34
B-1-8	1912	F_3	28	19–33	82	26.3±0.20	10.38±0.55
B-1-10	1912	F_3	26	19–27	151	23.1±0.10	7.75±0.30
B-1-12	1912	F_3	25	18–30	209	23.7±0.14	10.51±0.41
B-1-14	1912	F_3	25	19–29	56	21.8±0.14	7.18±0.46
B-3-5	1912	F_3	27	17–28	159	21.7±0.11	9.45±0.36
B-3-6	1912	F_3	28	16–27	229	22.5±0.09	8.71±0.27
B-3-8	1912	F_3	25	17–23	85	20.6±0.12	8.25±0.43

The Broadleaf variety is commonly grown in one section of the Connecticut Valley and is especially valuable for cigar wrappers. Sumatra which is an imported variety produces many leaves per plant but they are small. As may be seen from an examination of the table, the F_1 had an intermediate number of leaves. Segregation occurred in F_2 and selected F_2 plants gave F_3 families which differed in the average number of leaves. *B*-1-14, showed the lowest coefficient of variability of any F_3 family. Progeny of this same F_2 plant were also grown at another locality and they proved uniform in number of leaves, the calculated coefficient of variability being 6.44 ± 0.27. *B*–1–10 gave a low coefficient of variability and a mean leaf number which was about the same as in the F_1 generation, *i.e.*, intermediate between the parents.

A cross was studied between Connecticut Havana, which is grown as a wrapper and binder tobacco both in the Connecticut Valley and in Wisconsin, and Cuban, a variety commonly grown under shade. The parents and F_1 gave about the same number of leaves but in F_2 there was a great increase of variability, forms being obtained with a higher and lower leaf number than in either parent. The inheritance of size and shape of leaf was likewise investigated. The Cuban variety gives a short broad leaf and the Havana a longer leaf which is proportionally narrower than the Cuban. Lines were obtained in F_3 which bred true, respectively, to the parental leaf shapes.

East (1916*a*) has listed eight requirements, most of them independent mathematically, which should be met if size inheritance is typically Mendelian, when all populations succeeding the original cross are obtained by growing progeny of single self-fertilized plants. These are:

"1. Crosses between individuals belonging to races which from long continued self-fertilization or other close inbreeding approach a homozygous condition, should give F_1 populations comparable to the parental races in uniformity.

"2. In all cases where the parental individuals may reasonably be presumed to approach complete homozygosity, F_2 frequency distributions arising from extreme variants of the F_1 population should be practically identical, since in this case all F_1 variation should be due to external conditions.

"3. The variability of the F_2 population from such crosses should be much greater than that of the F_1 population.

"4. When a sufficient number of F_2 individuals are available, the grandparental types should be recovered.

"5. In certain cases individuals should be produced in F_2 that show a more extreme deviation than is found in the frequency distribution of either grandparent.

"6. Individuals from various points on the frequency curve of an F_2 population should give F_3 populations differing markedly in their modes and means.

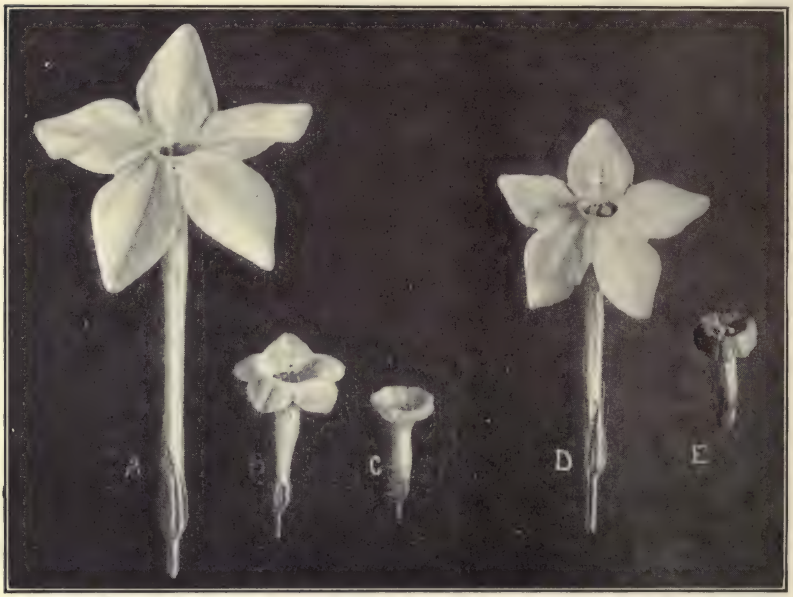


FIG. 36.—*A*, *N. alata grandiflora; B*, F_1 of *N. langsdorfii* × *N. alata grandiflora; C*, *N. langsdorfii* (1911); *D* and E, extremes of the F_2 generation (1912) × 3/8. (*After East.*)

"7. Individuals either from the same or from different points on the frequency curve of an F_2 population should give F_3 populations of diverse variabilities extending from that of the original parents to that of the F_2 generation.

"8. In generations succeeding the F_2, the variability of any family may be less but never greater than the variability of the population from which it came."

All of the above eight conditions have been obtained in experiments and no fact directly opposed to them has been discovered.

The quantitative characters in tobacco which have been studied are, therefore, typically Mendelian in their inheritance.

A list of these characters and of the authority for the inheritance is here given. Not all papers on this subject are included. Those given show the general behavior of many of the characters in inheritance.

TABLE XXXVIII.—INHERITANCE OF TOBACCO CHARACTERS AS SHOWN BY RESULTS OF CROSSES

Character	Grown in	Authority
Height of plant	F_1	Jensen, 1907.
Height of plant	F_1, F_2	Hayes, 1912.
Height of plant	F_1 to F_4	Howard, 1913.
Number of leaves	F_1 to F_3	Hayes, East, and Beinhart, 1913. Howard, 1913.
Leaf size	F_1 to F_3	Hayes, East, and Beinhart, 1913. Howard, 1913.
Leaf shape	F_1 to F_3	Howard, 1913. Hayes, East, and Beinhart, 1913.
Spread, length and diameter of corolla.	F_1 to F_3	Goodspeed, 1912, 1913. East, 1916*b*.
Sucker inheritance	F_1 to F_3	Johnson, 1919.
Base of leaf	F_1 to F_3	Howard, 1913

The results obtained in these studies of tobacco show that segregation occurs in F_2 for size characters and that forms similar to the parents as well as new sorts may be obtained in later generations.

Environment as a Factor in Tobacco Breeding.—It is a matter of common knowledge that environmental conditions widely modify the expression of characters. This is particularly noticeable in tobacco, where quality, size, and shape of leaf are of such marked importance. A belief has been frequently expressed that environment causes a breaking of type. The following quotation from Shamel (1910) emphasized this view for tobacco:

"The writer believes that the two efficient means of inducing variability as a source of new types are change of environment and crossing. So far as the writer is concerned, the change of environment—usually the growing of southern grown seed in the north—is the most effective means of inducing variability."

Statements of this nature have been used as evidence that environment modifies the characters of a pure line by inducing

variability. A careful survey of experimental studies does not support this contention. The development of the shade-grown tobacco industry in the Connecticut Valley is of interest in this discussion. This shade method first originated in Florida in 1896 and was tried experimentally in Connecticut through coöperation of the Connecticut Experiment Station and officials of the Bureau of Soils. In 1900 one third of an acre was grown and the crop sold at an average price of 72 cents per pound. A considerable acreage was grown in 1901 and the crop sold at public auction at a much higher price per pound. Indiscriminate introduction of unselected seed from Florida was practiced and in 1902 over 700 acres were grown under shade in Connecticut. The result was a disastrous failure, owing to a lack of knowledge of methods of handling and to the use of unselected seed. By further study of handling and through careful selection in which artificially self-pollinated seed was saved, the industry was placed on a firm foundation. This latter work was carried on by the Bureau of Plant Industry (Stewart, 1908). A knowledge of Cuban methods shows that imported Cuban seed is a mixture of many types. Some experiments have shown that the breaking up alluded to is an expression of the different hereditary qualities of the parental seed plants. In 1912 Hasselbring grew a number of pure lines of tobacco in Michigan which he had formerly grown in Cuba. No evidence of breaking up of type was observed and whatever changes occurred in a pure line, owing to the new conditions, were uniformly exhibited in all plants of the pure line. Similar conclusions were reached from the immediate introduction of individual seed capsules of different tobacco plants from Cuba and their subsequent growth under shade in Connecticut (Hayes, 1914). Careful studies at Pusa, India, convinced the Howards (1910*a*) that new conditions did not cause a breaking up of type. They ascribed the apparent variability of new introductions to cross-fertilization, which was shown to occur frequently in tobacco.

Although there have been some differences of opinion as to the cause of variability of new introductions, there is uniformity of belief regarding the methods of obtaining purity of type. Artificial self-pollination gives uniformity, and continued self-fertilization produces no harmful effects. This method was strongly recommended by officials of the United States Department of Agriculture (Shamel and Cobey, 1907) and by the different

state experiment stations. The Howards, in India, likewise urged the use of self-fertilized seed. Garner (1912) states that several types have been inbred by growing the seed under bag from six to eight years without any observable change in vigor or habits of growth. These facts, together with the studies of inheritance of quantitative characters, show that the pure-line theory and Mendel's law furnish a reliable guide to tobacco breeding operations.

As quality of cured leaf is of such great importance in tobacco, it is necessary that the breeder have a thorough knowledge of the sort of leaf desired. Practical breeding operations must then be carried on under the soil and climatic conditions in which the crop is to be grown. An added complication is the necessity of basing the final judgment of a particular selection upon the comparative value of the cured leaf after fermentation. The difficulties of comparing numerous strains, while not insurmountable, are naturally much greater than for an equal number of small grain selections.

Mutations in Tobacco.—The sudden appearance of giant plants with abnormally high leaf number has been recorded in the Sumatra, Maryland, Cuban, and Connecticut Havana varieties of *N. tabacum* (Allard, 1916). These new forms under field conditions have a much longer period of vegetative vigor than the normal varieties. Consequently blossoming does not take place under ordinary field conditions. Otherwise the general habit of each of these new types is not very different from the normal variety from which it was obtained.

Two of these new varieties of giant habit are of some commercial importance. A short account of their first recorded appearance together with their cultivation as commercial varieties will be given. Giant plants were noted in 1912 in the Cuban variety which is grown under shade in the Connecticut Valley. (Hayes and Beinhart, 1914). The history of the normal Cuban variety from which the giant type was obtained is of interest (Hayes, 1915). Seed of the normal variety was saved under bag, which insures self-fertilization, from 1904 to 1909 inclusive. In 1910 and 1911 seed was saved in bulk from plants which were grown under the cheese-cloth cover used in producing shade-grown tobacco, but individual plants were not bagged. During the period from 1904 to 1910 no abnormal types were observed. Studies of leaf inheritance in the Cuban variety were made from

1910 to 1914 inclusive. An average of 150 plants was carefully examined yearly and no aberrant types were observed.

In 1912 about 100 acres were grown by the Windsor Tobacco Growers' Corporation from seed saved in 1911, and late in the season three plants were discovered which had produced a high leaf number and showed no signs of blossoming. One of these plants when taken to the Connecticut Experiment Station greenhouse produced 72 leaves and blossomed about January first. Considerable seed was saved from this plant and one-third acre of the new type was grown in 1913. The plants were of uniform appearance. They differed from the normal Cuban in having leaves of a somewhat lighter green, in having but few basal suckers, and in a long continued period of growth; whereas the normal Cuban variety bears a terminal inflorescence after producing from 14 to 25 leaves on the main stem. From 25 to 30 acres have been grown yearly by the same tobacco company. The quality and yield of this giant variety which has been named Stewart Cuban, have been quite satisfactory. One of the great difficulties of growing these giant forms is the extra trouble of obtaining seed. This difficulty has been overcome in part by studies which show that a reduction of length of day leads to the production of blossoms. These studies will be briefly described after giving a short history of the Maryland Mammoth type.

The Maryland Narrowleaf Mammoth type first appeared in 1907 in the second generation of a cross between two common varieties of Maryland tobacco (Garner, 1912). One hundred and fifty-seven plants of this new form were grown in 1908 and all plants were of mammoth habit. This new variety has been grown commercially since that time and retains its characteristics of high leaf number and non-blooming habit under normal field conditions.[1] Accurate information regarding the acreage of Mammoth tobacco in southern Maryland is not available but some hundreds of acres were grown in 1920. The chief limiting factor in the acreage is the quantity of seed available. As Maryland tobacco is harvested by cutting and spearing the stalk, there is little additional cost in harvesting the giant type. The Mammoth variety will yield 2,000 lb. or more per acre and the

[1] Information kindly furnished by Dr. W. W. Garner, Physiologist, in Charge of Tobacco and Plant Nutrition Investigations, B. P. I., United States Department of Agriculture.

quality of cured leaf is superior to the ordinary varieties. Comparative yields show that the Mammoth variety yields 20 to 25 per cent. more than other varieties when grown on productive soil. As the Mammoth variety has shorter internodes than ordinary varieties the leaves shade one another. This prevents coarse texture and dark colors even on highly productive soil. The ordinary varieties, when grown on rich soils, yield dark-colored and coarse-textured leaves. The value per acre of the Mammoth tobacco is 30 to 40 per cent higher than ordinary varieties (see Fig. 37).

Garner and Allard (1920) have studied the effect of relative length of day on growth and development of plants, particularly with respect to sexual reproduction. By placing a ventilated, dark chamber in the field the relative number of hours of exposure to sunlight was controlled as desired. They found that:

"Normally the plant can attain the flowering and fruiting stages only when the length of day falls within certain limits, and, consequently, these stages of development ordinarily are reached only during certain seasons of the year. In this particular, some species and varieties respond to relatively long days, while others respond to short days, and still others are capable of responding to all lengths of the day which prevail in the latitude of Washington where the tests were made."

In the absence of a favorable length of day for bringing into expression reproductive processes in certain species, vegetative development may continue and thus lead to the production of such varieties as Stewart Cuban and Maryland Mammoth which under ordinary conditions never reach the flowering stage.

"Thus, certain varieties or species may act as early or late maturing, depending simply on the length of day to which they happen to be exposed."

The Stewart Cuban and Maryland Mammoth varieties of tobacco, as well as several other species were used in a determination of the effect of reduced length of day in forcing flowering. In discussing the effects of controlling light as a means of forcing flowering in Maryland Mammoth, Garner[1] says;

"Under a given length of day favorable to flowering, this type can be

[1] From a letter written September 14, 1920.

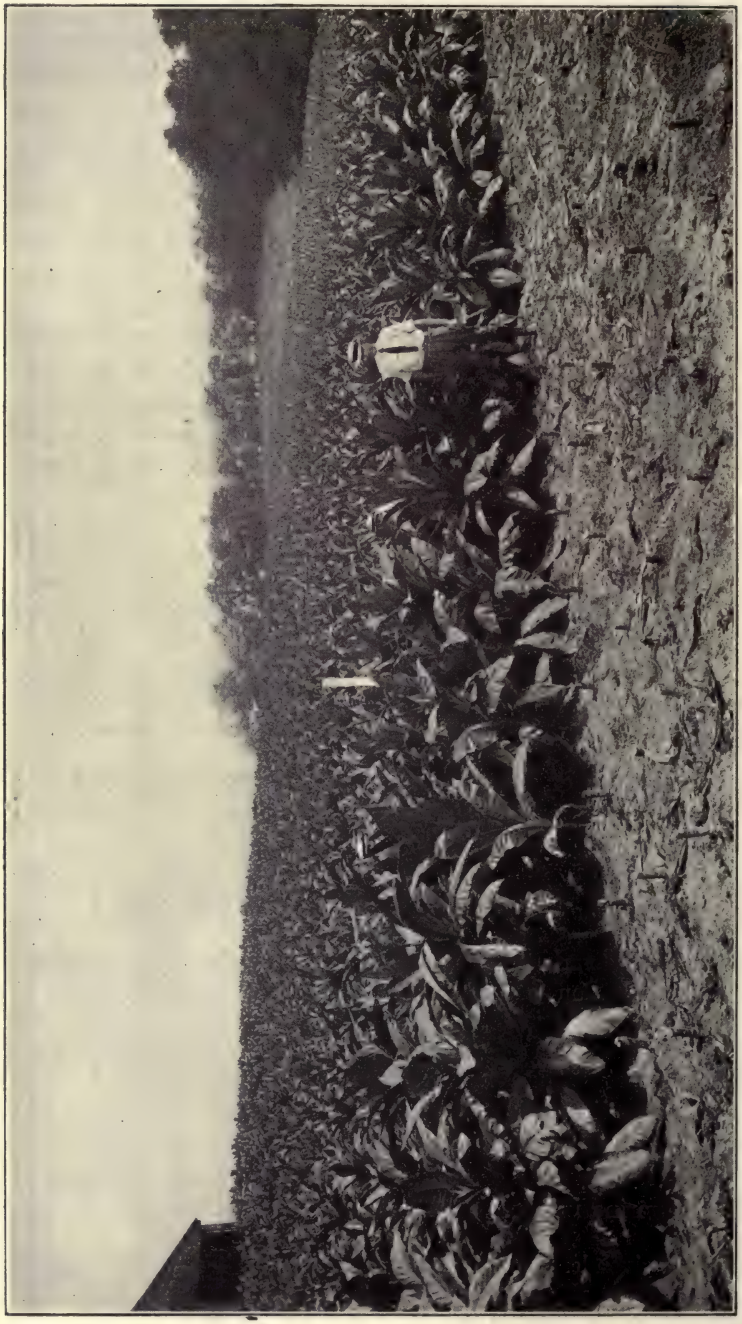


FIG. 37.—Field of Maryland Mammoth in Prince George's County, 1920. The man in the foreground is more than 6 feet tall. Two men of average stature standing in the tobacco are scarcely visible. The stake is 7 feet tall. (*Courtesy of Garner.*)

made to produce any quantity of seed ranging from a single pod up to a large inflorescence by appropriate regulation of the quantity of soil in which the plant grows."

Plants grown in 12-quart buckets produced large amounts of seed when the length of day was shortened by placing the plants in the dark chamber for a part of the normal day. A control series left out of doors during the experiment began to show flower heads about the middle of August (see Fig. 38). Plants exposed to seven hours of light daily produced large quanti-



FIG. 38.—Control series of Maryland Mammoth tobacco in twelve-quart buckets left out of doors during the experiment. Flower buds just beginning to show when photographed, August 19, 1919. (*Courtesy of Garner.*)

ties of seed while those exposed to twelve hours of light daily grew larger but were later in blossoming (see Fig. 39).

In southern Florida during the ordinary winter months, the Maryland Mammoth behaves as ordinary tobacco, showing no evidence of its tall late habit. Thus quantities of seed could easily be produced under these conditions.

Allard (1919) crossed normal varieties with the Mammoth type. The F_1 averaged somewhat higher in leaf number than the

normal varieties but invariably blossomed under field conditions in practically the same period as ordinary varieties of *N. tabacum.*



FIG. 39.—Front row in twelve-quart buckets exposed to light from 9 a.m. to 4 p.m. or 7 hours daily. Rear row in twelve-quart buckets exposed to light from 6 a.m. to 6 p.m. or 12 hours daily. Note that latter are larger plants but flowered considerably later than the former. (*Courtesy of Garner.*)

A total of 1820 F_2 plants was grown and 439 were of the giant habit.

CHAPTER XIII

COTTON AND SORGHUM[1]

Little is definitely known of the antiquity and origin of cotton. Evidence has been obtained which indicates that it was cultivated in India in 1,500 B.C. and in Egypt 1,300 years later. Species of cotton are indigenous both to tropical America and to India. Because of the extent of natural crossing (5–13 per cent.) (Balls, 1912) the difficulties of studying inheritance and of carrying on practical breeding operations are very great. It seems reasonable, however, to consider this crop in the self-fertilized group, as the extent of crossing leads to the belief that continued self-fertilization will not give harmful results. It also seems reasonable to conclude that deterioration in a selected variety is largely the result of natural crossing. Methods of pedigreed seed production should, therefore, be developed to their highest possible efficiency.

Classification and Inheritance.—*Gossypium* contains several species. The two species of cotton grown commercially in the United States, upland (*G. hirsutum*) and sea-island (*G. barbadense*) cross readily with each other. The varieties cultivated in Egypt also belong to *G. barbadense*, but in India the forms derived from *G. herbaceum* are chiefly grown. Webber (1905) was unable to cross Aiden cotton which he classified as *G. herbaceum*, with either sea-island or upland varieties. The commercial value of cotton and the separation into the above species groups is largely determined by three characteristics of the fiber: namely, length, tensile strength, and fineness. Other morphological characters have been used in classification. These are presence or absence of fuzz on the seed, color of fiber and flower, form of boll and general habit of growth. The wide range of environmental or place effect exhibited by the cotton plant generally, as well as heterozygosis due to natural crossing, has made clear-cut classification difficult. *G. hirsutum* is a vigorous annual plant with a

[1] While sorghum is botanically one of the grasses, yet from the standpoint of the breeder it is better treated with the self-fertilized group of crop plants.

branching upright stem and a tap root with numerous lateral branches. The leaves are alternate, 3 to 6 in. long, slightly less



FIG. 40.—Upper left, flower of Upland cotton, from below, with bracts removed showing the arrangement of calyx lobes, petals and nectaries; at right, petals; lower left flower of cotton with one bract removed showing spirally arranged stamens and stigma. (*After Cook.*)

in breadth, the lower ones being heart shaped, the upper more or less three- or five-lobed. The flowers are large and showy. The fruit develops into a pointed egg-shaped body about the

size of a small hen's egg and is closely filled with seeds. It is composed of from three to five cells. When ripe the boll turns brown and splits open and the lint and seed are exposed. The seeds, each about ⅜ in. long and half as wide, are covered with lint and fine fuzz. This lint, the cotton of commerce, is from ⅞ to 1½ in. long in the ordinary varieties. (Wilson and Warburton, 1919). *G. barbadense* is distinguished in part from *G. hirsutum* by its greater height, longer branches, longer and finer fiber, and seeds free from fuzz. Egyptian is generally considered a variety of *G. barbadense.* It is the variety grown largely in Egypt, also under irrigation in Arizona and southern

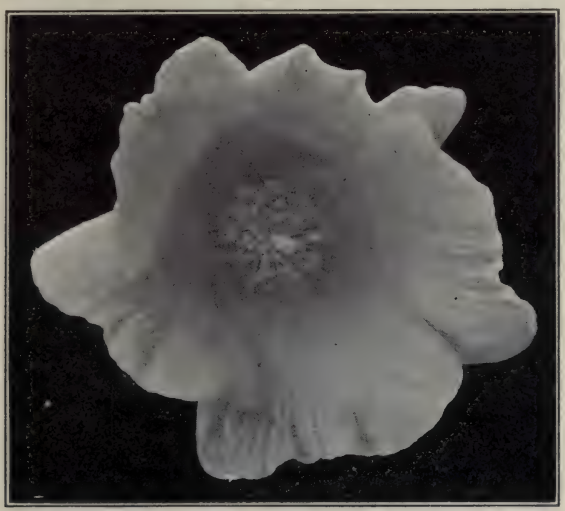


FIG. 41.—View of flower of cotton, from above, showing position of petals, stigmas and stamens (natural size). (*After Cook.*)

California. India cotton (*G. herbaceum*) has stems more slender than upland, and leaves with rounded lobes and smaller, less pointed bolls. The lint is white, yellow, or brown. Its cultivation is confined to southern Asia (Wilson and Warburton, 1919). Balls (1908, 1911, 1912) and Leake (1911) have investigated color inheritance of seed fuzz, lint, anthers, flowers, and sap. In most cases the second generation gave a mono- or di-hybrid ratio. On the other hand, ratios were also obtained which were not easily explained on a simple factor basis. The inheritance of the red spot on the petals of some varieties involves two factors with a 3:1:1:3 coupling. Red spot on the leaf showed simple mono-

hybrid segregation. In some crosses, studied independently by McLendon (1912) and Balls, between the dominant fuzzy-seeded and the recessive smooth-seeded forms, evidence was found of a single-factor difference as well as a two-factor difference. Balls also discovered that long fiber was dominant to short and that but one main factor difference existed. Likewise a dominant long petal crossed with a recessive short petal gave in the F_2 generation a 3:1 segregation. In a cross between Egyptian (Abassi) and Texas Upland, Balls obtained transgressive segregation in height of plants. Similar results were secured in studying the inheritance of date of flowering and weight of seed. The results of the study of weight of seed are of general interest.

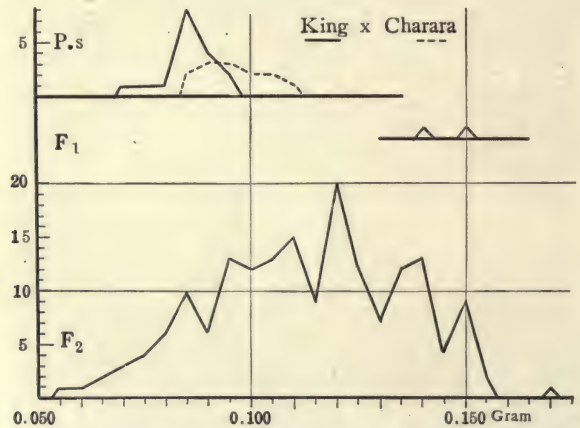


FIG. 42.—Seed weights of parent varieties, King and Charara, and F_1 and F_2 generation crosses. (*After Balls.*)

In a cross of Afifi and Truitt, where the mean seed weights of the parents were 0.105 g. and 0.135 g. respectively, the weight of the F_1 was 0.165 g. Weights in F_2 varied from 0.08 g. to 0.175 g. The light-seeded forms bred comparatively true in F_3 although differing somewhat in means. The larger-seeded types bred true in F_3 or segregated, giving both large-and small-seeded forms. An illustration of this sort of behavior for the parents, F_1 and F_2 generations, is given in figure 42 diagrammatically. As has been pointed out, length of lint is also inherited and in some cases segregation approaches a simple 3:1 ratio with long lint as the dominant character. Later generations in some crosses gave pure parental types as well as other lint lengths which appeared

homozygous. Correlation between length of lint and size of seed may explain some complications.

Mutations in Cotton.—The cotton plant, like *Œnothera*, has often been spoken of as having germinal instability and likely to produce mutations. While mutations undoubtedly do occur, it is likewise highly probable that many of the so-called mutations are simply segregates of a former natural cross. The ease with which natural crossing occurs and the large number of chromosomes (20 according to Balls) contained in the cotton gamete facilitate the appearance of forms differing from the general type. The larger the number of haploid chromosomes the more difficult it is to secure homozygous individuals after a cross. Egyptian cotton is described by Kearney (1914) as being a mutating type. From it the varieties Yuma, Pima, and Gila are supposed to have arisen. In this connection it is of interest to point out that the common belief as to the origin of Egyptian cotton is that it arose by hybridization between a brown-linted tree cotton and American sea island. The subsequent development is unknown.

In view of the foregoing and the fact that no convincing evidence has been presented to the contrary, the present writers believe that many of these supposed mutations are in reality factorial recombinations resulting from natural crossing.

Cotton Breeding.—Cotton improvement by breeding may be sought along lines similar to those followed with all naturally selfed crops. In producing pure-line material for scientific study and subsequent hybridization it is essential to obtain absolute self-pollination.

From a commercial standpoint, a productive cotton with long lint and smooth seed is desirable. Webber (1905) crossed Klondike, a productive upland variety, and sea island, which has long lint and smooth seed. Out of an F_2 generation consisting of several thousand plants, only 12 combined the large blunt bolls of the upland with the long lint and black seed of sea island. The progeny of each of these 12 plants was grown in isolated plots and subjected to vigorous selection. In the fifth generation a number of plants gave progeny "nearly fixed in type."

Resistance to wilt disease is a character of considerable commercial importance. This disease is caused by *Fusarium vasinfectum* Atk. which according to Orton attacks only the cotton and its near relatives. By the plant-to-row method and under wilt infection conditions, it was found possible to build up varieties

which are resistant to wilt. A number of resistant high-yielding varieties have been introduced in the cotton growing regions of the United States. The character of wilt resistance was transmitted in crosses but nearly every cross gave a different result. In general, resistance proved dominant but there was often considerable variability, possibly due to the gametic composition of the parents or to the nature of the reaction between the disease organism and the host plant or to the lack of uniform evironmental conditions. Wilt resistance does occur and varieties may be obtained which are resistant and are also of good quality with respect to yield and staple.

SORGHUM

Origin.—The numerous diversified forms of sorghum indicate that it has been cultivated a long time. Evidence has been found that it was grown in Egypt as early as 2200 B.C. Hackel places all the cultivated sorghums and the various forms of Johnson grass in one botanical species. It has been pointed out by Piper (1916) that two species exist—the perennials, Johnson grass and its varieties (*Andropogon halepensis*), and the annual sorghums (*Andropogon sorghum*). The former possesses rootstocks, and it is difficult to cross it with either the cultivated or wild forms of sorghum.

The wild annual sorghums, which are found almost exclusively in Africa, cross readily with the cultivated forms. Africa is thought to be the native home of our cultivated sorghums.

Classification and Inheritance.—On the basis of the three economic characters—production of grain, sugar, and broom-straw—three distinct types of sorghums have been developed. All of these produce forage and some of them, as Sudan grass, are grown primarily for this purpose. Piper, after Ball, has suggested a group classification for all the forms of *A. sorghum*, cultivated in America, to which the student is referred (Piper, 1916). Only a brief statement will be given here. Small-stemmed sorghums, such as Sudan-grass and Tunis-grass, comprise one group. The other group, the large-stemmed sorghums, are divided on the basis of the character of the pith—whether it is juicy or dry. The juicy sorghums may be either sweet or slightly sweet to sub-acid. The dry sorghums are further classified into varieties on the basis of panicle characteristics. Hilson (1916) found that a pithy stalk was dominant

to a sweet stalk. The second generation of the cross segregated as a monohybrid. Graham (1916) of India, studied the inheritance of length of glume and color of seed-coats in some natural and artificial crosses. Long and short glumes behaved as a simple Mendelian pair with the former dominant. In the inheritance of color of grain a series of multiple allelomorphs are involved. Red may be allelomorphic to yellow or white and likewise yellow may be allelomorphic to white. The usual color dominance is shown. Sometimes when yellow and white are crossed the heterozygote is red and in the next generation segregates with a 9 red : 3 yellow : 4 white ratio. Graham suggests that certain of the white seeds are undeveloped reds requiring the presence of yellow to cause the development of the red color.

Some Results of Selection.—Sorghum improvement by breeding has been accomplished principally through selection. Dwarf forms have occurred in most varieties and have furnished material for the production of such varieties as Dwarf Milo, Dwarf Kafir, etc. These varieties have been isolated through selection. Sugar content has also been improved. Failyer and Willard conducted selection experiments at the Kansas Station from 1884 to 1903. During that time they increased the sugar content of the Orange variety from 12.62 to 16.10 per cent. At the Delaware Agricultural Experiment Station even more striking results were obtained (Neale, 1901). The variety Amber, from which selections were made, contained on the average 11 per cent. sugar with a purity of 65. One of the selections made from it had a sugar content of 18.2 per cent. with a purity of 81. Dillman (1916), of the United States Department of Agriculture, made several selections from Minnesota Amber with the object of securing an early maturing, drought resistant strain. One of the selections, Dakota Amber, has proved valuable. It is more dwarf in habit of growth than Minnesota Amber and matures 15 days earlier. It produces excellent forage as well as abundant seed. Early dwarf forms, as a rule, are more drought resistant than late ones.

Method of Breeding Sorghum.—Sorghum belongs to the naturally self-fertilized group of farm crops and the essential features of breeding it are the same as for the group. However, sorghum is more frequently cross-fertilized than most of the other naturally selfed crops and for this reason it is necessary to resort to bagging the panicles, where different lines are grown in close proximity to one another. That bagging does not inhibit

the setting of viable seed is shown by the work of Connor, Ball, Ten Eyck, Townsend, and Leidigh, all of whom secured viable seed from panicles so protected. Leidigh (1911) credits Connor with the statement that, "a particular strain of Orange sorghum which he grew two generations from seed, bagged each year, possessed extraordinary vitality and vigor and was remarkably pure and uniform." Townsend (1909) obtained similar results. From the foregoing facts it is evident that sorghums should be bred as a self-fertilized crop. Bagging the panicles is a necessary precaution where different lines are grown near one another.

By means of roguing chance mixtures and crosses are eliminated and varieties are kept in a pure condition. The isolated seed plot also is recommended as a correct farming practice.

CHAPTER XIV

MAIZE BREEDING

Maize was the most important bread crop of the American Indians and even today is the most important crop in the western hemisphere. The Indians brought the culture of maize to a high state of advancement and developed innumerable varieties. On the foundations made by the Indians modern corn-breeding has made marked advances, but perhaps no North American varieties are so notable as those developed by the Incas in Peru.

Origin and Species.—It is generally believed that Mexico is the original home of the maize plant, although there is no absolute proof of this (Harshberger, 1897). *Zea mays* L., belongs to the tribe Maydeæ of the order Gramineæ. All varieties of Indian corn are placed in the species *mays*. The nearest relative of maize is teosinte, *Euchlæna mexicana* Schrad. Teosinte and maize cross readily and a natural hybrid between these cultivated grasses was described under the name *Zea canina* by Watson (Harshberger, 1904). A study of these crosses led Harshberger (1904, 1909) to make the hypothesis that maize originated from a hybrid between a sport of Euchlæna and normal teosinte. Montgomery (1906) reached the conclusion that maize and teosinte had a common progenitor. It was considered likely that the ancestral form of these cultivated grasses was a large much-branched grass "each branch being terminated by a tassel-like structure bearing hermaphrodite flowers." As evolution progressed, the lateral branches of maize came to bear only pistillate flowers and the central branch staminate flowers. This theory is strengthened by the types of inflorescence which frequently appear in maize varieties. Often the central spike of the tassel of lateral branches bears seeds, while the side branches of the same tassel bear only staminate organs. All gradations appear between the normal ear of maize and the staminate tassel. It is not uncommon in self-fertilized maize races to obtain plants in which the tassel of the main branch bears both male and female

organs. These various abnormalities tend to support the hypothesis outlined by Montgomery.

Collins (1912) has supported the hypothesis that maize originated as a hybrid between teosinte and an unknown grass belonging to the tribe Andropogoneæ. This grass is believed to be somewhat like some varieties of pod corn (*Zea mays tunicata*) which produce seeds only in the tassel and are in many essential characters strongly contrasted with teosinte. These conclusions have been reached after extensive studies of many primitive varieties of maize, teosinte, and hybrids between teosinte and maize. Collins especially emphasizes the fact that "in practically every case where there is pronounced divergence between teosinte and pod corn, maize shows characters of an intermediate nature and these characters are usually variable."

Kuwada (1919, abstract by Ikeno, 1920) has published cytological support for this theory. He finds the chromosomes of maize to be of two types, long and short. He also finds that Euchlæna has 10 haploid chromosomes which are long, and Andropogon likewise has the same number of haploid chromosomes which are distinguished by their shortness.

Sturtevant (1899) divided the species *Zea mays* into several groups and considered each of specific rank. The more common practice is to make the five major groups sub-species, retaining the monotypic species *Zea mays*. This plan was followed by East (see East and Hayes, 1911). A short description of the differential characters of these five groups is given here.

Zea mays tunicata, the pod corns, Sturtevant, *Bulletin* Torrey Botanical Club, 1894, page 355.

"In this group each kernel is enclosed in a pod or husks, and the ear thus formed is enclosed in husks." This is perhaps the least deserving of sub-specific rank as it is an unfixable group (see page 189).

Zea mays indurata, the flint corns, Sturtevant, *Bulletin* Torrey Botanical Club, 1894, page 355.

The group comprises those varieties with a starchy endosperm in which the soft starch is surrounded by corneous starch. The proportions of soft and corneous starch vary considerably in different varieties.

Zea mays everta, the pop corns. Sturtevant, *Bulletin* Torrey Botanical Club, 1894, page 325.

In this group there is only a small proportion of soft starch

in the endosperm and a correspondingly large proportion of corneous starch. Some seeds may be entirely free from soft starch, but there is generally some soft starch surrounding the germ. The group is characterized by the small size of its seeds and ears.

Zea mays indentata, the dent corns. Sturtevant, *Bulletin* Torrey Botanical Club, 1894, page 329.

The corneous starch in this group is located at the sides of the seed and the soft starch extends to the summit. The soft starch dries more rapidly than the corneous and this produces the shrinkage which causes the characteristic indentation of the seed.

Zea mays amylacea, the soft or flour corns, Sturtevant, *Bulletin* Torrey Botanical Club, 1894, page 331.

This group is recognized by an almost entire absence of corneous starch. There is no indentation in some varieties and only a slight one in others. The soft starch content characterizes this group.

Zea mays saccharata, the sweet corns. Sturtevant, *Bulletin* Torrey Botanical Club, 1894, page 333.

"A well-defined species group characterized by the translucent, horny appearance of the kernels and their more or less crinkled, wrinkled, or shriveled condition." East (1910*d*) presented evidence which shows that the sweet corns are dent, flint, or pop varieties which have not the ability to mature starch normally. The few starch grains produced are small, angular, and imperfect.

INHERITANCE OF CHARACTERS

Endosperm Characters.—The word xenia was first used by Focke (1881) to denote the effect which was apparently produced by the action of pollen upon the maternal tissue of the seed. The endosperm of maize was cited as a classical example of such an effect. After the discovery by Guignard (1899) and Nawaschin (1898) that the polar nuclei of the endosperm fuse with the second male nucleus of the pollen grain, De Vries (1899), Correns (1899), Webber (1900), and Guignard (1899, 1901) saw that this furnished an explanation of xenia in maize. From a consideration of inheritance of endosperm character the following law of xenia may be formulated:

Xenia may result from crossing varieties which differ in a single visible endosperm character. When a character difference is dependent on a single dominant factor, xenia occurs only when the factor is carried by the male parent, or, when dominance is incomplete, xenia results when either variety is the male. When a character difference is dependent on more than one factor, all located in one parent, and dominance appears complete, xenia occurs only when these differential factors are located in the male; when dominance is incomplete, xenia occurs if the factors are located in either parent. When two varieties have a similar character or a different character expression but contain between them endosperm factors necessary for the production of a new character, xenia occurs when either variety is the male.

The inheritance of an intermediate starchy-sweet (called pseudo-starchy) condition, which is often present in some sweet corn ears, has been studied by Jones (1919). Three factors were shown to explain the results: (1) a plant factor, *A*, necessary for complete expression of the so-called pseudo-starchy character; (2) an endosperm factor, *B*, which prevents the characteristic shrinking of sweet seeds; (3) an endosperm factor, *C*, determining opaqueness. *C* gives complete dominance, while *A* and *B* give an intermediate condition when heterozygous, and *B* in addition shows a cumulative effect in proportion to the number of factors involved. *C* and *c* give the greatest differential effect only in the presence of the homozygous condition for *A* and *B*. From this brief discussion it is easy to see that reciprocal crosses between *AABBcc* × *aabbCC* will not give like results. *AABBcc* fertilized with *aabbCC* will give an endosperm condition *ABBbcC*, while the reciprocal cross will give *abbBCc*. As *A* is necessary for recognizable expression of pseudo-starchiness, one cross will show xenia while its reciprocal will not.

The following endosperm characters have been studied and the results are briefly summarized. (See Table XXXIX.)

The cross between the waxy variety of Chinese maize and American sweet varieties is of interest, as in F_1 maize with a corneous endosperm was obtained, while in F_2 a ratio of 9 horny to 4 sweet to 3 waxy seeds was obtained. Many starchy-sweet crosses have been studied and as yet no case has been obtained which showed more than a single main factor difference. Apparently the sub-species, *Z. mays saccharata*, differs by only a single main factor from the starchy subspecies.

TABLES XXXIX.—SUMMARY OF INHERITANCE OF ENDOSPERM CHARACTERS OF MAIZE

Parents	F_1	F_2	Authority
Chinese Maize (waxy) × American Maize (sweet).	Horny	Ratio of 9 horny to 4 sweet to 3 waxy.	Collins and Kempton (1911) (1914).
Starchy (flint, dent, or pop) × Sweet.	Starchy	3 starchy to 1 sweet.	Correns, 1901. East and Hayes, 1911.
Yellow × Colorless endosperm.	Completely dominant or intermediate yellow. Absence of color in cross studied by White.	3 yellow to 1 white. 15 yellow to 1 white. 3 white to 1 yellow.	Correns, 1901. East and Hayes, 1911. White, 1917.
Aleurone color: purple, red, or white.	Dominance or partial dominance of color usually. Sometimes dominance of colorless.	Ratios indicate from 1 to 5 differential factors.	East and Hayes, 1911. East, 1912*b*. Emerson, 1912*a*. Emerson, 1918.
Flour Maize × Flint	No immediate effect.	Ratio 1 flour seed to 1 flint seed on each F_1 ear.	Hayes and East, 1915.
Flour × Pop.....	No immediate effect.	Segregation, but more complex than in flint-flour cross.	Hayes and East, 1915.
Normal × Defective Seeds.	Normal	Segregation on a 3 : 1 or more complex ratio.	Jones, 1920.

Reciprocal crosses between flour and flint showed no immediate effect of cross-pollination. The ears, however, of the F_1 plants showed a distinct segregation into flour and flint seeds in a 1 : 1 ratio. Later generations showed that the results were most easily explained on the cumulative factor basis. If a soft flour variety was pollinated by a flint race, the endosperm would contain two factors for soft flour, *SS*, and one for flint condition, *F*, or *SSF*. The reciprocal cross would be *FFS*. If two factors, *FF* or *SS*, are completely dominant over one factor, *S* or *F*, respectively, there would be no immediate effect of cross-pollination and the segregation on F_1 ears would be in a 1:1 ratio. Dents crossed with flour races give a very similar result, but the seeds are not so easily distinguished by inspection. Reciprocal crosses between pop and flour races show no immediate effect of pollination with complex segregation on the ears of F_1 plants. Pure flour and pop forms may be obtained in later generations, but the results cannot be explained by a single factor difference. With the hypothesis that pop and flour corns differ by two or more main factors and with each factor behaving in a some-

what similar manner as in the flint-flour cross, the difficulty of a correct classification by inspection is apparent.

The endosperm of corn may be either yellow, pale yellow, or white. In some crosses there is almost complete dominance of the yellow color, while in other crosses the F_1 is intermediate or pale yellow. The results of most yellow-white crosses may be explained by one factor or by two multiple factors. It is impossible to tell by inspection whether a particular yellow variety contains one or two factors for yellow. The only sure method is

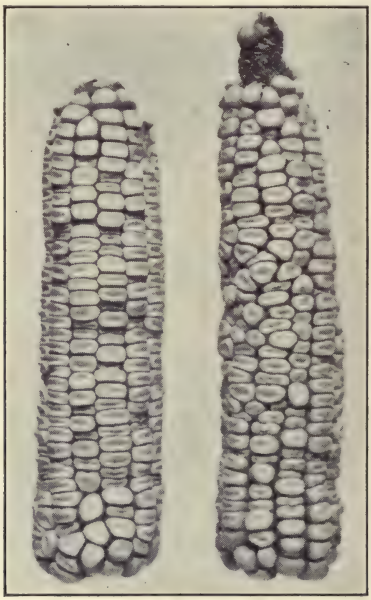


FIG. 43.—Two first year self-fertilized ears of Minn. No. 23 showing the lethal endosperm character.

to note whether the segregation approaches 3:1 or 15:1. White (1917) has recorded a cross in pop corns between yellow and white endosperm varieties in which white is the dominant character. The results were explained by supposing that the white variety carried an inhibitory factor, A, and also a factor for yellow or Y, while the zygotic condition of the yellow variety was YY.

The inheritance of aleurone color is even more complex than the inheritance of yellow endosperm color. The aleurone may be either colorless, mottled, red, or purple. Three factors are

necessary for the production of red aleurone. These Emerson (1918) has called *R*, *C*, and *A*. In addition to these three factors, *Pr*, in either the simplex or duplex condition, gives purple aleurone. An inhibitory factor which was called *I* was first discovered by East and Hayes (1911). When this is present, the aleurone layer is colorless. Races of white corn exist which contain some but not all of the factors necessary for the production of aleurone color. Certain crosses between white races give colored aleurone. With five or six factors involved, it becomes apparent that segregation in certain cases may be in a simple 3:1 ratio, while segregation in other crosses may give extremely complex ratios. There are various intensities of the purple color in different races. These have been discussed in detail by Emerson (1918). Over waxy or floury endosperm purple aleurone gives a dull black appearance. With a variation in color of the endosperm from white to dark yellow there is a corresponding variation in color of the aleurone from purple to brownish shades. These differences in aleurone appearance are due to the inheritance of other genetic factors for endosperm characters beside those which govern the ability to produce aleurone color. There are some genetic differences in aleurone colors which are not related to the underlying endosperm characters. Two color patterns have been mentioned by Emerson under the names speckled and dark-capped. The color is found on the crown of the seed and varies from a mere speck to a large spot. Both color patterns are recessive to normal or self-color. Aside from these color patterns which are apparent in homozygous races, there are mottled colors which are only obtained in the heterozygous condition. Emerson has given quite conclusive proof that mottling is associated with the *Rr* factor pair. Apparently endosperms of the constitution *RRR* or *RRr* are self-colored while *Rrr* shows mottling.

PLANT CHARACTERS

Colors in Plant Organs.—There is a group of anthocyan color characters which are expressed in one or all of the following organs: cob, pericarp, silk, tassel, *i.e.*, glume, and in the leaves and stems. There are several different character expressions of a stable nature for this group of color characters. In some cases the color in two or more organs may be inherited as if due

to a single factor. For example, the color in cob and pericarp is often correlated in inheritance. Emerson (1911) has found a case in which the factor for color in the cob behaves as an allelomorph of the factor for color in the pericarp. In the illustration given in Table XL R_1 represents the factor for cob color and R_2 the factor for pericarp color.

TABLE XL.—SUMMARY OF A CROSS IN WHICH A FACTOR FOR COB COLOR BEHAVED AS AN ALLELOMORPH OF A FACTOR FOR COLOR OF PERICARP

Parents			F_1			F_2 Zygotes	Appearance	
Zygote	Gametes	Appearance	Zygote	Gametes	Appearance		Cob	Pericarp
R_1R_1	R_1	Red in cob	R_1R_2	R_1 or R_2	Red cob, red pericarp	1 R_1R_1	Red	White
R_2R_2	R_2	Red in pericarp				2 R_1R_2	Red	Red
						1 R_2R_2	White	Red

East and Hayes (1911) have given a case of a cross between two reddish blush pericarp colors which developed only under light conditions, which gave a 15 : 1 ratio in F_2. This indicates two separately inherited factors.

There are numerous expressions of colors. Hayes (1917) obtained four pericarp colors which bred comparatively true when self-fertilized. These were called solid red, in which the pericarp was uniformly red; variegated, in which the color was in deep red stripes of various sizes; pattern, in which the color was also in stripes but was much lighter in intensity; colorless, lacking color in the pericarp. The factors for red, variegated, pattern and colorless appeared to form a series of multiple allelomorphs. The cross between pattern and variegated gave an increase in bud sports in F_1, *i.e.*, ears which produced two sorts of pericarp color sharply differentiated; while in F_2 a few solid red ears were obtained and many striped ears. This was presented as an instance in heterozygous material in which a change in a character occurred. Without attempting an explanation it was pointed out that no such change occurred in six generations of selection in self-fertilized families of the red, striped, or pattern lines. Emerson (1914*a*, 1917) has studied the inheritance of these anthocyan colors for several years. To explain the production of solid red in variegated races, he supposes a change or mutation

in the factor *V*, for variegated, to *S* for self-color. Emerson concluded:

"That these results favor the idea that single allelomorphic factors, rather than two or more closely linked factors, are responsible for the color pattern of both glumes and pericarp."

The concluding paragraph of Emerson's 1917 paper is directly in line with the ideas which have been developed throughout this book. With most plant-breeding material of our farm crops, there is no evidence for basing a system of plant improvement upon mutations, as these are infrequent. With anthocyan color characters of corn, inherited changes sometimes occur more frequently and such mutations become of selection value. This does not invalidate the pure-line conception for the large number of cases where factor stability is the rule. To quote from Emerson:

"The existence of the series of at least nine or ten multiple allelomorphs to which variegation belongs, indicates that a factor for pericarp color has mutated several times. Some of the factors for this series have not been observed to mutate, while others have mutated rarely and still others many times. In fact, the principal difference between certain of the factors is thought to lie in their relative frequencies of mutation."

Podded Condition.—The podded character was thought by East and Hayes (1911) to be a simple dominant and to be dependent on a single factor for its development. Extracted recessives bred true to the podless condition. Collins (1917) has presented evidence which indicates that the ordinary type of tunicate maize represents a case of imperfect dominance and that it, like the Andalusian fowls, is unfixable and related to the heterozygous condition. Selfed seeds of typical podded ears produced three types of plants: (1) like the parent; (2) with normal ears; (3) a plant which does not produce seed in the lateral inflorescences but in perfect flowers in the tassels. Jones and Gallastegui (1919) obtained similar results. A starchy tunicate ear was used as the female parent and was pollinated with pollen from a non-tunicate sweet race. The linkage between the starchy and tunicate factors was quite close, only 8.3 per cent. of crossing-over occurring.

Auricle and Ligule.—Emerson has shown that the absence of auricle and ligule is a recessive character. In a cross between a

pure race for the absence of these characters and a normal variety all F_1 plants had normal leaves. In F_2, ratios of 672 normal-leaved plants to 221 liguleless were obtained.

Chlorophyll Inheritance.—Numerous abnormalities for chlorophyll development have been observed in corn, many of which behave as simple recessives giving a 3:1 ratio in the F_2 of a cross between the normal and abnormal form.

Lindstrom (1918) has reviewed earlier investigations of chlorophyll inheritance and has made a careful genetic study of several different chlorophyll abnormalities. Three of these—white, virescent-white, and yellow—appear in the seedling stage. The white form is a true albino, apparently lacking chloroplasts. The virescent-white appears white at first, but under favorable conditions it gradually becomes a yellowish green color, especially at the tips of the leaves. There is considerable variation in the appearance of different seedlings of this type but genetically all behave alike. The yellow type gives seedlings with a yellow color. Both the white and the yellow seedlings die before maturity.

The normal green form behaves as an allelomorph to the various seedling abnormalities and contains the three dominant genes, *W*, *V*, and *L*. Counts of the number of normal green plants and the three seedling types obtained from various heterozygous plants are as follows:

Green	1,513	White	555
Green	4,297	Virescent-white	1,394
Green	1,493	Yellow	532

Virescent-whites which turned green on maturity were selfed and produced a progeny consisting of 717 virescent-white seedlings and nine green. The latter were due probably to stray pollen.

From a study of interrelation of these various factors, Lindstrom has concluded that the following phenotypic formulas explain the appearance of different sorts of seedlings;

Green	Virescent-white	Yellow	White
LVW	*LvW*	*lvW*	*LVw*
lVW			*Lvw*
			lVw
			lvw

These studies have considerable bearing on the present

conception of inbreeding and cross-breeding as applied to corn improvement. Lindstrom found, for example, that plants containing the *wW* combination were less vigorous than *WW* forms. As a rule, a *Ww* plant produced only a single stalk which was easily blown over in a strong wind.

There are also abnormal chlorophyll types which appear in the mature plant. Of these, golden, green-striped, fine-striped, and japonica types are simple Mendelian recessives to normal green. In the golden type, when a month or more old, the green color begins to disappear. The golden type is not very vigorous toward maturity. It produces abundant pollen and small ears. The green-striped form appears about two months after germination. These stripes are uniform in distribution, green and lighter areas alternating, and running parallel through the leaf. Mature green striped plants are less vigorous than normal green forms and the leaves wilt more severely on hot days. The japonica types are striped with green, pale yellow, yellow, and white, and are well known, being frequently used for ornamental planting. These forms are more vigorous than the golden or green-striped types. There are also fine-striped and spotted forms. The spotted forms have not as yet been studied thoroughly.

Four of the mature plant chlorophyll types have been found to be recessive to the normal green forms. The following genetic factors have been used by Lindstrom:

g — golden type
st — green-striped
j — japonica
f — fine-striped

The following summary expresses the factorial condition of these forms of chlorophyll abnormality;

Chlorophyll types	Chlorophyll factors
Green	*WVLGStJF* or *WVlGStJF*
White	*wVLGStJF*
Virescent-white	*WvLGStJF*
Yellow	*WvlGStJF*
Golden	*WVLgStJF* or *WVlgStJF*
Green-striped	*WVLGstJF*
Japonica white-striped	*WVLGStjF*
Japonica yellow-striped	*WVlGStjF*
Fine-striped	*WVLGStJf*

Studies of the linkage relations of these chlorophyll factors have been made. The seedling factors *w* and *v*, and *v* and *l* show independent inheritance. The factors which influence the chlorophyll development in the mature plant, *g* and *st*, *g* and *j*, *g* and *f*, *j* and *st*, *j* and *f*, appear to be inherited independently. Also *st* and *v* are inherited independently.

The linkage relations suggest that one pair of chromosomes in maize contains the factor pairs *Gg* and *Ll* as well as the aleurone factors, *Rr*. The japonica striping is influenced by the aleurone factor *R*, as the presence of *R* represses striping, while *r* allows full expression of the pattern. These abnormalities have been discussed in some detail as they show typical Mendelian inheritance of chlorophyll characters and have considerable bearing on the improvement of corn by the isolation of pure biotypes.

Some Seed and Ear Characters.—Crosses between dents and flints were studied by East and Hayes (1911). There is no immediate visible effect of foreign pollen on the endosperm seed characters which separate these subspecies. Segregation occurred in F_2; some forms were obtained in F_3 which bred true to flint habit; some bred true to the dent type; while still others showed segregation. Two or more factors were necessary to explain results. The inheritance of the pointed condition of the seed which is characteristic of white rice pop was also studied by Hayes and East (1915). It was found possible to transfer this pointed condition to the dent subspecies. Results were complex and indicated that two or more cumulative factors were involved.

Size Characters.—Emerson and East (1913) summarized inheritance of size characters of seeds and ears. Weight of seed, seed measurement, number of rows, and length and diameter of ear were characters studied. In general, the F_1 condition was intermediate, and complex segregation occurred in F_2. The inheritance of height of plant, of period of maturity, and of suckering habit, was also studied. The fact that a considerable series of fairly stable varieties is known which exhibit numerous conditions of the development of particular size characters, is also evidence of a complex inheritance. Segregation occurred in F_2 and extracted forms were obtained which approached the original parental conditions. Intermediates, as well as extremes, sometimes bred true.

Chemical Composition.—The classical selection experiments of the University of Illinois for the purpose of isolating high and low protein, and high and low oil strains, are well known. They prove conclusively that strains differing in chemical composition may be isolated by selection. Table XLI gives the results for 15 years' selection. This information was obtained through the kindness of Professor L. H. Smith.

Progress during the latter years of the experiment has not been so rapid as during the early years, which is probably because the genetic limit for high and low protein and high and low oil pro-

TABLE XLI.—A. RESULTS OF SELECTING MAIZE FOR HIGH AND FOR LOW PROTEIN CONTENT RESPECTIVELY

Average Percentage Protein in Crop Each Generation

Year	High strain	Average for period	Low strain	Average for period	Difference	Difference for period
1896	10.92		10.92			
1897	11.10		10.55		0.55	
1898	11.05		10.55		0.50	
1899	11.46		9.86		1.60	
1900	12.32	11.37	9.34	10.24	2.98	1.12
1901	14.12		10.04		4.08	
1902	12.34		8.22		4.12	
1903	13.04		8.62		4.42	
1904	15.03		9.27		5.76	
1905	14.72	13.85	8.57	8.94	6.15	4.91
1906	14.26		8.64		5.62	
1907	13.89		7.32		6.57	
1908	13.94		8.96		4.98	
1909	13.41		7.65		5.76	
1910	14.87	14.07	8.25	8.16	6.62	5.91
1911	13.78		7.89		5.89	
1912	14.48		8.15		6.33	
1913	14.83		7.71		7.12	
1914	15.04		7.68		7.36	
1915	14.53	14.53	7.26	7.74	7.27	6.79
1916	15.66		8.68		6.98	
1917	14.44		7.08		7.36	
1918	15.48		7.13		8.35	
1919	14.70		6.46		8.24	

B. Result of Selecting Maize for High and for Low Oil Content Respectively

Average Percentage Oil in Crop Each Generation

Year	High strain	Average for period	Low strain	Average for period	Difference	Difference for period
1896	4.70		4.70			
1897	4.73		4.06		0.67	
1898	5.15		3.99		1.16	
1899	5.64		3.82		1.82	
1900	6.12	5.41	3.57	3.86	2.55	1.24
1901	6.09		3.43		2.66	
1902	6.41		3.02		3.39	
1903	6.50		2.97		3.53	
1904	6.97		2.89		4.08	
1905	7.29	6.65	2.58	2.98	4.71	3.67
1906	7.37		2.66		4.71	
1907	7.43		2.59		4.84	
1908	7.19		2.39		4.80	
1909	7.05		2.35		4.70	
1910	7.72	7.35	2.11	2.42	5.61	4.93
1911	7.51		2.05		5.46	
1912	7.70		2.18		5.52	
1913	8.15		1.90		6.25	
1914	8.29		1.98		6.31	
1915	8.46	8.02	2.07	2.03	6.39	5.99
1916	8.50		2.08		6.42	
1917	8.53		2.09		6.44	
1918	9.35		1.87		7.48	
1919	9.05		1.77		7.28	

duction has nearly been obtained. These new strains have been named Illinois High Protein, Illinois Low Protein, Illinois High Oil, and Illinois Low Oil respectively. The high and Low Protein strains were crossed with a normal Leaming variety by Hayes (1913*a*). The F_1 generation of the cross between Low Protein and Leaming produced approximately the same protein content as Illinois Low Protein, while the cross between Leaming and Illinois High Protein gave about the same protein content in F_1 as the normal Leaming variety. Results are given in Table XLII.

TABLE XLII.—INHERITANCE OF PROTEIN IN THE FIRST GENERATION CROSSES BETWEEN ILLINOIS LOW PROTEIN AND ILLINOIS HIGH PROTEIN AND STADTMUELLER'S LEAMING

Variety	Number of ears analyzed	Variation in ears in protein content	Average protein content, dry basis
Illinois High Protein	19	11.95–17.10	14.87
Leaming, 1910 seed	13	7.75–16.28	11.85
F_1 Cross	12	9.25–14.68	11.85
Illinois Low Protein	16	6.81–11.56	9.41
Leaming, 1911 seed	14	8.21–15.94	12.19
F_1 Cross	9	7.69–11.86	9.18

Self-fertilization seems a logical means of obtaining pure races of different chemical compositions. Numerous ears should be self-fertilized and analyzed. Those that appear of promise may then be used and their breeding nature determined by the progeny test. As soon as homozygous forms containing the desired characters have been isolated, they may be used as foundation stock for the production of an improved variety. That high protein races may thus be isolated has been shown by Hayes and Garber (1919).

TABLE XLIII.—PROTEIN CONTENT OF SELFED STRAINS OF MINNESOTA NO. 13 AND CROSSES BETWEEN THEM

Strain No.	Average protein content		
	1916	1917	1918
1	15.82	14.03	15.10
4	14.47	13.06	14.93
Normal No. 13		10.17	10.25
1 × 4 F_1 Ear *A*			12.25
1 × 4 F_1 Ear *B*			12.44
1 × 4 F_1 Ear *K*			12.81

These same workers showed that there was a correlation between the number of seeds produced by particular self-fertilized F_1 ears of the crosses *A*, *B*, and *K*, and protein content. Low number of seeds per ear was correlated with high protein content. The F_1 crosses, *A*, *B*, and *K*, yielded slightly more than normal

corn and gave 2.5 per cent. higher protein content. These particular strains, 1 and 4, were not examined during the seedling stage and consequently it was not then known that strain 1 was heterozygous for the white seedling chlorophyll abnormality which Lindstrom has designated by the factor *w*. In the second generation grown from self-fertilized ears of *A*, *B*, and *K*, approximately one-fourth of the seedlings were pure white. Lindstrom has shown that plants heterozygous for the chlorophyll factors *Ww* are slightly less vigorous than homozygous green forms. These facts lead one to expect that high protein races with good yielding ability may be produced. On the other hand,



FIG. 44.—Two high protein strains of Minn. No. 13 at left and right respectively which have been self-fertilized for five years and first generation cross between them in the center. The F_1 yielded slightly more than normal Minn. No. 13 and analyzed 2½ per cent. higher in protein content.

maximum yield of grain and high protein content probably can not be obtained in the same variety.

CORN IMPROVEMENT BY THE TRAINED PLANT BREEDER

A uniform technic has been developed for the small-grain breeder. With corn, however, the correct method of breeding is even yet somewhat problematical. Investigations have helped to clarify our ideas regarding the value of different methods of work. For the farmer the results obtained have tended to simplify previous ear-to-row methods. For the technical breeder, however, the application of Mendelian principles has resulted in several plans, some of which appear rather complex. Their

justification apparently rests on a firm genetic foundation. As yet practical demonstrations of improvement in corn by the application of Mendelian principles are unavailable.

Relation of Ear Characters to Yield.—Corn shows have accomplished much in teaching growers the characteristics of various standard varieties. They have, however, over-emphasized the value of ear type as a means of corn improvement. Much work has been carried on with the view of determining the relation between various ear and plant characters and ability to give high yields. In general, no single character has been found to be so closely related with yielding ability as to be of much value from the standpoint of selection. Too close uniformity of type probably tends to reduce yield, for we have learned that self-fertilization in corn causes a marked decrease in growth vigor as compared with cross-fertilization.

For the purpose of illustrating the general nature of results in this field, the work of Williams and Welton (1915), in Ohio, may be used. They compared the yields of ears selected on the basis of wide differences of type. In the majority of cases selection was continuous, *i.e.*, long ears from the long strain and short ears from the short strain. Summarized results are given in Table XLIV.

TABLE XLIV.—RELATION BETWEEN EAR CHARACTERS AND YIELD

Characters worked with	Length of test, years	Differences in yield, bu.	
Long *vs.* short ears	10	Long	1.39
Cylindrical *vs.* tapering	9	Tapering	1.65
Bare *vs.* filled tips	8	Filled	0.34
Rough *vs.* smooth dent	7	Smooth	1.76
High *vs.* low shelling percentage	6	Low	0.42

These differences are very small considering that the yields obtained averaged between 60 and 70 bu. per acre. Although continuous selection isolated strains which differed considerably from each other, the yields were not markedly affected. The progressive change in shelling percentage of the progeny was most striking and illustrates how corn may be modified by selection (see Table XLV).

TABLE XLV.—SHELLING PERCENTAGE AS AFFECTED BY CONTINUOUS SELECTION

Year	Shelling percentage in crop harvested	
	High	Low
1910	84.73	83.67
1911	87.30	84.66
1912	85.34	77.86
1913	87.09	76.93

The results presented in Table XLIV do not justify the belief that selection for ear type is a means of improving yield. Other experiments (Olson *et al*, 1918) have given results of a similar nature.

Ear-to-Row Breeding.—Corn is very largely cross-pollinated, therefore selection under normal conditions considers only the mother plant. The ear-to-row method has been considered as the quickest means of isolating an improved variety. It was first introduced by Hopkins (1899) at the Illinois Experiment Station. As East (1908) pointed out, the method has some difficulties which have been partly obviated by improvements in technic. The improvements consisted of replication; *i.e.*, duplication of rows from the same ear in different parts of the field; and of an attempt to overcome the harmful effects of too close inbreeding. The method outlined by Williams (1905, 1907) was to plant one-half the seed of each ear that was used for the ear-to-row test. The remnants of those ears which excelled by the progeny test were planted and the progeny intercrossed. Another feature of Williams' plan was to influence several breeders to work with the same variety. New blood was then introduced into the ear-to-row plot of each breeder every fourth or fifth year from a grower who was using the same breeding method. The difficulties of the method are that a yearly plot is needed for the ear-to-row test, an isolated plot for the crossing of the remnants, a multiplication or seed plot, and the general field. Montgomery (1909) suggested a plan which obviates some of these difficulties. This plan is to grow an ear-to-row plot only once in several years, and in the intervening years use a bulk seed plot planted by the hill method, selecting only from the vigorous stalks in perfect stand hills (see Chapter XIX). A review of the literature on ear-to-

row breeding seems unnecessary. It seems sufficient here to point out that there are no experiments which show conclusively that continued ear-to-row breeding may be expected to give a significantly higher yield than seed produced by the seed-plot method. Ear-to-row breeding with a variety that has not been systematically selected is doubtless the most rapid means available to the corn farmer for the isolation of better yielding hereditary combinations. As an illustration of the sort of results usually obtained, the results of a five years' study as carried on at Nebraska (Kiesselbach, 1916) are given in Table XLVI.

TABLE XLVI.—EFFECT OF EAR-TO-ROW BREEDING ON THE YIELD OF HOGUE'S YELLOW DENT, AT THE NEBRASKA STATION, 1911–1915

Description	Yield in bushels per acre					
	1911	1912	1913	1914	1915	Average
Original Hogue's Yellow Dent...	42.6	51.6	9.8	62.8	79.5	49.3
Continuous ear-to row selection.	44.0	52.9	7.7	65.3	76.8	49.3
Increase from single ear-to row strain.....	38.2	45.6	7.3	55.0	75.3	44.3
Increase from composite four ear-to-row strains.....	42.5	54.6	12.1	63.5	80.0	50.5

These studies with Hogue's Yellow Dent were started in 1902. This variety was selected because of its yielding ability as shown by varietal test. Apparently no method of selection has given very strikingly beneficial results.

Home-Grown Seed.—The value of using home-grown seed of a variety which has shown its yielding ability by competitive test is well known to most corn growers. Nebraska results may again be used for illustrative purposes.

TABLE XLVII.—EFFECT OF ACCLIMATIZATION ON CORN

Character of seed	Yield in bushels per acre
Show corn from Illinois, Indiana, and Ohio (5 varieties).....	39.8
Seed from growers in state (5 varieties).....	45.6
Local varieties near experiment station (7 varieties).....	48.8

The data presented in Table XLVII show that home-grown seed usually yields better than seed brought from a distance. A

system of broad breeding, the use of a high-yielding, adapted variety, and the storage of the seed so that it will germinate vigorously are important practices which should be a part of each corn-breeder's plan.

Relation between Heterozygosis and Vigor.—In an earlier chapter the effects of self-fertilization in corn were discussed



FIG. 45.—Minn. No. 13 self-fertilized high protein strain No. 1. This strain has dark green leaves, medium sized ears and the tassels are somewhat scantily provided with pollen.

and the hypothesis outlined that vigor in F_1 crosses was due to the partial dominance of linked growth factors. This question is of considerable importance from the standpoint of the corn breeder. The subject will be discussed under the following headings:

1. Immediate effect of crossing on size of seed.
2. F_1 varietal crosses.
3. Isolation of homozygous strains.

Immediate Effect of Crossing on Size of Seed.—The question of immediate effect of crossing on size of seed has received considerable attention, and Carrier (1919) has recently considered this a main cause for the conflicting results of corn experiments. He demonstrated the fact that mixtures of seed of different strains gave higher yields than seed of a single strain and explained the results on the basis of increased yield due to the increased weight of the endosperm of varietal crosses as compared with normally pollinated seeds within a variety.

Other investigations have partially supported Carrier's contentions. Studies of the effect of pollen of a different strain or variety on endosperm development are given in Table XLVIII.

TABLE XLVIII.—IMMEDIATE EFFECT OF POLLINATION ON ENDOSPERM WEIGHT

Number of tests	Number in which weight of crossed seed exceeds that of normal seed	Number in which weight of normal seed exceeds that of crossed seed	Average percentage of increase due to immediate effect of foreign pollination	Authority	Method
5	5	0	8.8	Collins and Kempton, 1913	Mixture of pollen of same and different variety.
31	23	8	2.8	Wolf, 1915	Mixture of pollen of same and different variety.
2	2	0	19.2	Jones, 1918	Selfed strains and crosses between them.

These results show that there was an immediate effect of pollen on the weight of the endosperm of crossed seed compared with that produced by intra-varietal pollination. In varietal tests, however, as conducted by the plot method, the degree of crossing between different varieties would not usually be over 50 per cent. Averaging the results of Wolf and of Collins and Kempton gives about 5 per cent. increase due to crossing. Reducing this by half gives an error in varietal tests of not more than 2.5 per cent. as a result of increased endosperm development due to the immediate effect of foreign pollen. As the studies of Collins and

Kempton were made with widely different varieties, the results are probably somewhat more striking than if more closely related forms had been used.

F_1 Varietal Crosses.—The utilization of hybrids as a means of obtaining more vigorous types was urged by Beal (1876–1882). Since then there has been frequent mention of the vigor of F_1 crosses, and Morrow and Gardner (1893, 1894) outlined a plan for the production of crossed corn seed. Renewed interest in this subject was aroused as a result of the publications of East



FIG. 46.—Minn. No. 13 high protein strain No. 4. Short, erect strain with light green leaves. Produces good ears. Tassels are plentifully supplied with pollen.

(1908*b*) and Shull (1908, 1909) on the effects of inbreeding and cross-breeding, and of Collins (1909, 1910) on the value of first generation hybrids in corn. Many experiments in which first generation crosses have been compared with their parents have been made. In Table XLIX only those varietal crosses are used in which the F_1 has been compared with both parents.

A careful study of this table shows that first generation crosses, on the average, yield more than the average of their parents. In many cases the cross exceeds the higher yielding parent. No

TABLE XLIX.—FIRST GENERATION CROSSES BETWEEN CORN VARIETIES

Authority	Location	*A*	*B*	*C*	*D*	*E*	*F*	*G*	Method of test and remarks
Hartley, *et al*, 1912	Chico, Cal.	16	4	12	− 2.5	13	3	+ 7.7	Single row plots. Female parents unadapted, males adapted.
Hayes and East, 1911	Mt. Carmel, Conn.	3	2	1	+ 1.8	3	3	+28.0	Male parents adapted, females unadapted.
Collins, 1910*a*	Lanham, Md.	16	12	4	+16.6	14	2	+53.0	Widely different types. Single plot of 16 hills.
Collins, 1910*b*	Washington, D. C.	10	7	3	+25.6	8	2	+81.0	Sweet corn. Single plots.
Morrow and Gardner, 1892	Champaign, Ill.	5	3	2	+ 7.0	5	0	+14.0	Adapted varieties. Single plot tests.
Morrow and Gardner, 1893	Champaign, Ill.	4	2	2	− 1.2	3	1	+ 7.7	Adapted varieties. Single plot tests.
Hayes, 1913*a*	Mt. Carmel, Conn., 1912	19	10	9	− 3.5	16	3	+10.1	Adapted varieties, one replication, single row plots.
Hayes, 1913*a*	Mt. Carmel, Conn., 1913	8	5	3	+ 5.3	5	3	+ 8.3	Adapted varieties. One plot of three rows each.
Hartley, *et al*, 1912	Sherman, Waco, Corsicana, Tex.	11	4	7	− 0.1	10	1	+ 9.8	Adapted varieties. Single row plot. Average of test in three localities.
Belling, 1912*b*	Florida	1	1	..	+43.7		..	+48.0	Adapted varieties. Single plot tests.
Williams and Welton, 1915	Ohio	7	5	2	+ 0.3	7	6	+ 3.2	Adapted varieties. Single plot tests.
Jones, *et al*, 1917	Mt. Carmel and Storrs, Conn.	17	9	8	− 0.2	14	3	+ 6.2	Adapted varieties. Single plot tests. Average of two localities.
Jones, *et al*, 1917	Mt. Carmel, Conn.	12	9	2	+ 4.2	11	1	+16.3	Adapted varieties. Single plot tests.
Hutcheson and Wolf, 1917	Blacksburg, Va.	4	1	3	−11.2	3	1	+ 4.3	Adapted varieties. Four-row plots. Two replications.
Kiesselbach, 1916	Lincoln, Neb.	10	..	..			..	− 1.9	Adapted varieties. All late varieties.
Kiesselbach, 1916	Lincoln, Neb.	3	..	..			..	+ 1.2	Adapted varieties. Crosses between early and late varieties.
Hayes and Olson, 1919	Univ. Farm, St. Paul, Minn.	11	10	1	+11.7	10	1	+14.5	Adapted varieties. One replication, three-row plots. Average results of two to four years.

A. Number of crosses tested.
B. Number of crosses yielding more than better parent.
C. Number of crosses yielding less than better parent.
D. Average percentage increase or decrease as compared with better parent.
E. Number of crosses exceeding yield of average of parents.
F. Number of crosses yielding less than average of parents.
G. Average percentage increase or decrease as compared with average of parents.

general rule can be given and the only sure means of determining the value of a cross is by the experimental test. Results have shown that F_1 crosses between good yielding varieties which differ from each other in several characters frequently yield considerably more than either parent and more than pay for the trouble of producing crossed seed. Thus the tests made in Con-



FIG. 47.—F_1 cross of Minn. self-fertilized strains No. 1 × No. 4.

necticut (Jones *et al*, 1919) and those carried out in Minnesota (Hayes and Olson, 1919) showed that F_1 crosses between selected eight-rowed flints and dents very frequently exceeded either parent in yielding ability. For each growth character in which the parent varieties differ there is usually an intermediate condition in F_1. There is a tendency for a partial dominance and the first generation often exceeds the average of the parents in most

of its characters. F_1 crosses are of value from the standpoint of earliness. Thus a cross, studied at Minnesota in 1919, between Squaw flint and Minnesota No. 13, approached the dent parent in height of plant and the flint parent in earliness and exceeded both in yield. Such a cross would be of much value as a silage or husking variety under northern conditions.

The production of crossed seed is not very difficult. The varieties to be crossed may be planted in alternate rows and the tassels removed from one variety before any of the pollen has matured. Seed produced by the detasseled variety is known as first generation crossed seed. If the varieties to be crossed differ in maturity they should be planted at different times so that both bloom at about the same date.

Isolation of Homozygous Strains.—Shull (1908, 1909) first suggested the utilization of crosses between self-fertilized strains as a means of increasing yield in corn. Such crosses often give very high yields. The chief objections to this method are that self-fertilized strains are usually of very low yielding capabilities and that the seeds from selfed lines are usually much smaller than from normally pollinated corn. Even though crosses between self-fertilized lines yielded very vigorously, the method has not seemed commercially desirable. Low yields of seed per acre would increase the cost of seed. Under unfavorable conditions the food supply of the seed might not give the young F_1 plant a vigorous start. Jones (1918) has made a suggestion which removes some of these objections. After isolating selfed strains, tests are made to determine which four biotypes are most desirable as parents. Suppose these are numbered 1, 2, 3, and 4 respectively. Numbers 1 and 2 are crossed, also 3 and 4, by detasseling all of one biotype in each group. Seed from the plants of each detasseled biotype is then planted in alternate rows in an isolated plot and all of one combination, as 3×4, detasseled. Seed from these detasseled rows is used for commercial planting.

This method seems worthy of more extensive trial. Such a cross was compared at the Connecticut station with the best dent variety obtained from a varietal survey followed by a variety test. The highest yielding dent variety gave a yield of 92 bu. while the cross under similar conditions yielded 112 bu.

Every investigator who has produced self-fertilized strains of corn has been impressed by the large number of undesirable

abnormalities which are isolated. These abnormalities through ordinary seed selection are not eliminated from the commercial variety. Self-fertilized strains, however, stand or fall upon their

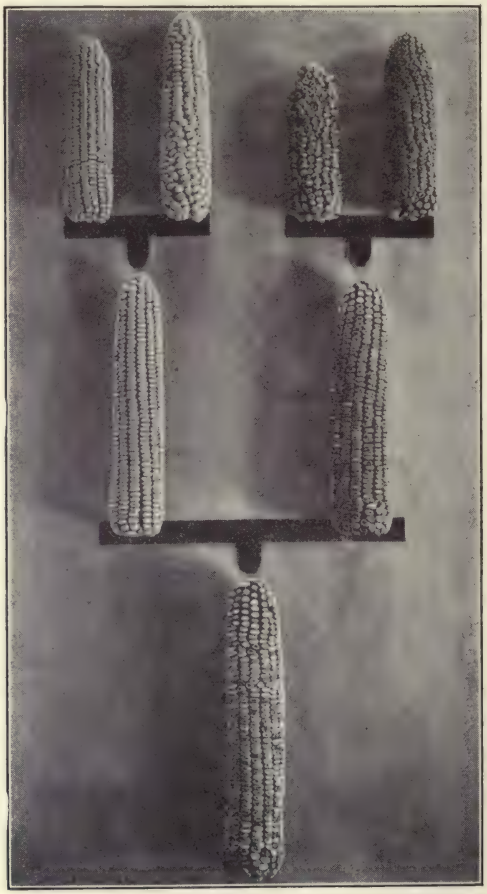


FIG. 48.—Average yields of 4 self-fertilized corn strains above; F_1 crosses in the center; the double cross below. (*After Jones.*)

own merits. Through self-fertilization the unfavorable strains may be eliminated. Crossing of the more desirable strains followed by selection seems a logical method for synthetically producing improved maize varieties.

CHAPTER XV

GRASSES, CLOVER, AND ALFALFA

The importance of hay crops in the world's agriculture makes desirable their consideration from the standpoint of improvement by breeding. Grasses, clover, and alfalfa differ strikingly in (see Chapter III) amount of seed set when artificially self-pollinated. Red clover (*Trifolium pratense*) is practically self-sterile; white clover (*Trifolium repens*) sets few seeds when protected from insect pollination; timothy (*Phleum pratense*) under a bag produces few seeds; and brome grass (*Bromus arvensis*) under the same conditions sets seed abundantly. Although common alfalfa (*Medicago sativa*) and yellow alfalfa (*M. falcata*) cross freely, seed of either may be produced by selfing. Enough examples have been cited to show that there are not only differences in the modes of pollination in the three mentioned classes of hay crops but also differences within each class. Carefully controlled experiments with grasses to determine the percentage of naturally crossed and naturally self-fertilized seed are very limited. To what extent decrease in vigor will result from artificial self-pollination is also an unanswered question. When self-sterility is not a limiting factor, the methods of breeding all these crops are essentially alike. The ease with which some of them may be clonally reproduced has led to slight modifications in breeding technic. In the following brief discussion, the aim has been to choose a few examples rather than to enter into an exhaustive treatment of the entire field.

GRASSES

Timothy ranks far ahead of the other grasses in importance. Some of the other hay grasses which may be mentioned are orchard grass (*Dactylis glomerata*), tall oat-grass (*Arrhenatherum elatiŭs*), and brome grass (*Bromus inermis*). These three grasses are adapted to certain conditions better than is timothy. Some important pasture grasses are Kentucky bluegrass (*Poa praten-*

sis), Canada bluegrass (*Poa compressa*), and redtop (*Agrostis palustris*).

The variability (see Fig. 49) of each of the different species of grasses presents a wealth of material for breeding purposes.



FIG. 49.—Individual timothy plants grown under like conditions. The upper plants are undesirable, one having weak stems and the other lacking vigor. The lower plants are more desirable. They differ in density of plant and number of culms. (*Courtesy of Myers.*)

Moreover, the fact that many of them may be conveniently propagated as clones facilitates a study of the value of individual

FIG. 50.—Flowers of timothy.

1. Spike.
2. Floret—*a*, anther; *b*, filament; *c*, branched stigma; *d*, style; *e*, ovary; *f*, outer glume.
3. Outer glume.
4. *a*, feathery stigma; *b*, style; *c*, ovary.
5. Spikelet showing *a*, palea; *b*, floral glume. (*After Beal after Trinius and Scribner.*)

Size: 1, $\frac{4}{5}n$; 2, 80*n*; 3, 4, 5, greatly enlarged.

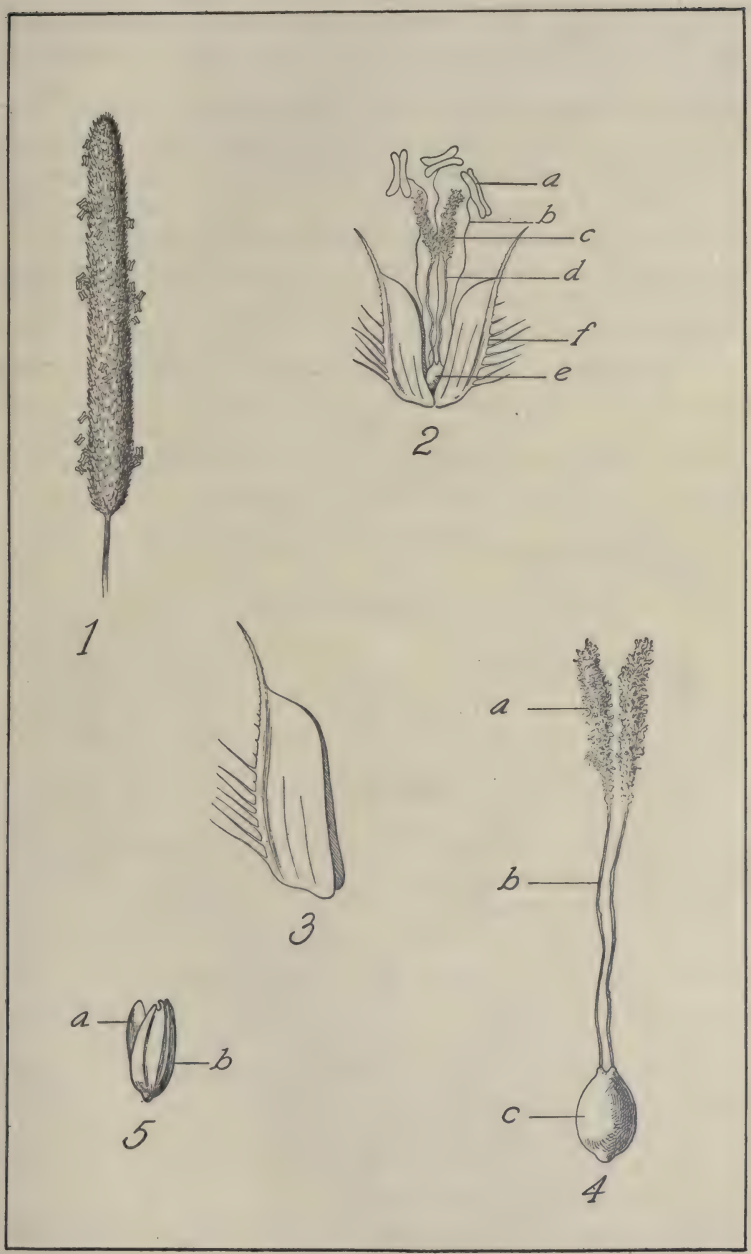


FIG. 50.

plant selections. The hereditary constancy of forms so isolated may be tested by selfing or by adopting methods which insure close breeding.

Breeding Timothy.—The United States Department of Agriculture has carried on extensive experiments in timothy breeding at New London and North Ridgeville, Ohio, but unfortunately the work has not been published. As a result of breeding, two improved varieties have been widely distributed through the Ohio Experiment Station. The Cornell and Svalöf Experiment Stations have done considerable timothy breeding.

Webber *et al* (1912) published a detailed report of the experiments as carried on at Cornell. Samples of timothy seed were procured from various sources in the United States, Canada and other countries. This seed produced an abundance of different forms from which selections were made. Individual plants were selected on the basis of the following characters;

1. High-yielding ability.
2. Height.
3. Broad and thick plants, which stool abundantly.
4. Many and dense culms.
5. Erect, non-lodging plants.
6. Many large leaves.
7. Leaves extending well toward the top of the plant.
8. Leaves remaining green until plant is nearly ready to harvest.
9. Rust resistance.
10. Spikes of medium size, setting seed freely.

The ultimate aim was to produce a high-yielding variety. A selected plant was dug up and vegetatively propagated by separating bulblets from it. The bulblets were set out in rows (16 to 24 per row) and allowed plenty of space for individual development. Self-fertilized seed from these various clones was planted in sterilized soil and the seedlings were transplanted in rows as above. By a comparison of these rows and the respective clones from which they came it was found whether they were breeding true for the characters desired. When sufficient seed was available, plots were sown broadcast and yields obtained. As soon as a form appeared valuable and bred comparatively true, it was isolated and increased.

According to Webber self-fertilized seed may be produced by placing several spikes of the same plant, just before blooming, under a paper bag. At University Farm Minn., only a few seeds

were obtained by this method. Another method is sometimes used in clonally propagated rows. Each row is surrounded by a fence about 10 ft. high made of finely woven cloth. This method does not prevent some cross-pollination but it does bring about a high degree of inbreeding. A tall growing crop, such as rye, surrounding isolated plots prevents pollination with undesirable strains or varieties.

As would be expected in dealing with a heterozygous crop, the self-fertilized seed of the various isolated clones produced plants which showed considerable difference in their inheritance. Some of the clones bred fairly true when reproduced by selfed seed, others did not. Table L, taken from Webber *et al* (1912), illustrates the transmission of yielding ability in some clones.

TABLE L.—TRANSMISSION OF YIELD IN TIMOTHY BY CLONAL AND SEED PROPAGATION

Number of original plant	Plat No.	Average yield per plant of mother by clonal propagation (ounces)	Plat No.	Average yield per plant of progeny by self-fertilized seed propagation (ounces)
		LIGHT-YIELDING PLANTS		
12.07	1,797	1.005	3,216	2.121
9.03	1,713	1.830	3,109	3.364
104.30	1,794	1.982	3,213	4.071
191.19	1,785	2.283	3,142	3.143
811.02	1,728	2.542	3,166	1.925
128.19	1,799	2.462	3,217	0.966
211.31	1,792	2.806	3,211	1.905
212.36	1,653	2.811	3,143	4.140
8.04	3,011	2.941	1,959	3.714
107.30	3,033	3.158	1,960	1.182
		HEAVY-YIELDING PLANT		
271.26	1,660	13.521	3,152	11.455
887.10	1,620	13.783	1,905	7.600
875.30	1,752	13.811	3,182	7.915
224.15	1,619	14.133	1,904	9.000
860.30	1,744	14.517	1,934	7.636
820.27	1,740	15.587	3,206	10.844
860.25	1,743	15.970	1,931	9.428
889.31	3,189	16.000	3,190	9.043
245.28	1,796	16.308	3,215	9.457
37.31	1,630	20.274	3,122	7.636

The practical results which have been attained by this method of breeding are brought out in Table LI, also taken from Webber *et al.*

TABLE LI.—SUMMARY, SHOWING YIELD OF FIELD-DRY HAY

	Yield in pounds per acre	
	1910	1911
Average yield of 17 new varieties	7,451	7,153
Average yield of 7 checks	6,600	4,091
Actual average increase	851	3,062



FIG. 51.—View of vegetatively propagated row plots of timothy. Each plot is propagated from a single, original plant. Note that the two central plots are comparatively late in maturity; also note differences between these two strains, one having erect culms and heads, the other having somewhat spreading culms and long loose heads. (*Courtesy of Piper.*)

The season of 1911 was particularly unfavorable for the growth of timothy. The new varieties gave a greater increase that year than in the preceding and more favorable one. Webber *et al* attribute this difference partly to the rust resistance of the new strains.

The method of breeding timothy at Svalöf as reported by Witte (1919) is not essentially different from that practiced at

Cornell. Individual plant selections are vegetatively propagated in plots isolated as much as possible. Seeds produced by the better clones are planted in varietal plots for comparison. The best commercial varieties are also grown for comparison. When a new variety proves superior and has practical uniformity, it is increased and distributed on a large scale. A comparison of ordinary timothy and two improved forms distributed by the Svalöf Station is shown in Table LII (Witte, 1919).

TABLE LII.—YIELD OF DIFFERENT VARIETIES OF TIMOTHY IN TRIALS AT SVALÖF, 1909–1918

Variety	Kilograms of green fodder per hectare			
	First year's lay	Second year's lay	Total	Yield per cent. compared to ordinary Swedish timothy
Svalof's Gloria	14.48	11.03	25.51	120.6
Svalof's Primus....	13.46	10.21	23.67	111.9
Ordinary Swedish..	11.57	9.59	21.16	100.0

Timothy, like many other grasses, is susceptible to a rust (*Puccinia graminis*). It has already been mentioned that in making selections at the Cornell Station some attention was given to resistance to this fungus. Eleven of the better Cornell selections have been tested for rust resistance (Hayes and Stakman, 1919). The relation of other characters to resistance was also studied. The rust classes are; 1, no rust; 2, slight infection; 3, moderate infection: and 4, heavily rusted. Average erectness is taken with 1 as a basis of an erect plant and 10 a procumbent one. Table LIII presents the data.

From the table it is apparent that the Cornell selections possess a high degree of resistance. Relatively few plants are found in rust classes 3 and 4. The Minnesota selections show the reverse condition, *i.e.*, most of the plants are found in classes 3 and 4. These facts show that a variety of rust-resistant timothy may be isolated.

Timothy breeding may be briefly summarized as follows:

1. Individual plants propagated vegetatively in rows. Bulblets are placed far enough apart in the row to give ample room for individual development.

2. The clones produced in 1 are closely inbred or seed is saved from vegetatively multiplied plants in isolated plots. By

TABLE LIII.—RUST RESISTANCE IN TIMOTHY IN RELATION TO OTHER CHARACTERS AS SHOWN BY VARIOUS DATA

Variety	Rust classes				Rust mean	Average yield per plant, lb.	Erectness mean	Average length of head, cm.	Average height, cm.	Average numbers of stools
	1	2	3	4						
Cornell 1,611.....	80	11	1	0	1.1	1.0	2.3	11.9	88	122
Cornell 1,620.....	77	26	3	2	1.3	1.0	2.2	18.3	88	138
Cornell 1,630.....	79	15	9	2	1.3	0.9	3.1	12.3	85	141
Cornell 1,635.....	61	14	9	3	1.5	0.8	2.9	11.4	85	109
Cornell 1,671.....	56	13	13	5	1.6	0.8	2.9	11.6	89	123
Cornell 1,676.....	87	10	3	6	1.3	0.9	2.9	13.1	87	116
Cornell 1,687.....	86	12	9	6	1.4	0.9	3.7	11.3	88	131
Cornell 1,715	90	11	6	3	1.3	0.8	3.0	10.3	86	98
Cornell 1,743.....	100	3	12	7	1.4	1.0	5.6	10.9	84	134
Cornell 1,777.....	36	0	4	0	1.2	0.9	5.7	11.5	83	142
Cornell 3,230.....	32	5	5	0	1.4	0.9	3.1	12.9	86	117
U. S. Dept. Sel. 1...	2	12	70	40	3.2	0.6	2.6	13.0	91	64
U. S. Dept. Sel. 2...	4	4	19	13	3.0	0.8	3.3	10.9	87	90
U. S. Dept. Sel. 3...	0	7	15	9	3.1	0.8	2.8	13.3	92	72
L. L. May Sel. 1....	2	3	24	15	3.2	0.6	2.3	12.4	86	70
L. L. May Sel. 2....	8	5	25	6	2.7	0.6	3.1	10.1	80	92
Griggs Bros. Sel. 1..	1	1	15	5	3.1	0.7	3.0	12.8	86	91

planting the seed so produced clones are tested for transmission of the desired characters and also for uniformity.

3. When sufficient seed is available, plots are sown broadcast and tests for yield are obtained under ordinary field conditions.

4. A selection which has shown performance ability is increased in isolated plots and distributed to the farmers.

CLOVERS

The importance of clovers as forage crops and their rôle in soil improvement make them of great economic value. *Trifolium pratense,* or ordinary red clover, is by far the most widely grown. Alsike clover (*T. hybridum*), because it may be grown in more acid soil than the other clovers, is favored in certain localities. Some of the other clovers are white (*T. repens*), crimson (*T. incarnatum*), and the sweet clovers (*Melilotus alba* and *M. officinalis*). All of these species are biennial or perennial except *T. incarnatum,* which is an annual.

Red Clover.—It has been demonstrated several times that the species *T. pratense* will set practically no seed when protected from the visit of insects, particularly bumblebees. However, this is not the only factor which influences fertilization. Westgate *et al* (1915) found that moist soil and atmospheric condi-

tions induced the formation of a large percentage of infertile ovules. All the cells remained sporophytic, no reduction taking place with the formation of an embryo sac. As much as 100 per cent. ovule infertility was found in the first clover crop. The rate of pollen tube growth was shown to be much slower in self- than in cross-pollinated plants. It is probable that pollen-tube growth is too slow to effect fertilization when the plant is selfed. The pollen of red clover is easily burst by an excess supply of moisture. Martin (1913) demonstrated that good artificial germination of pollen could be obtained on membranes which were just moist enough properly to regulate the supply of water to the pollen. He suggests that the stigma of red clover performs the same function as the membranes.

The above facts necessitate a method of breeding which is essentially a restricted form of mass selection. Before starting selection it is desirable to make comparisons of the varieties produced by other breeders and of commercial seed from different sources to obtain the best form for further breeding operations. A seed plot may then be used, in which each plant is spaced so that its characters may be determined. Undesirable plants should be removed before pollination. By repeating this process, forms with the desired characteristics and with practical uniformity may be isolated.

Selection for Disease-Resistant Clover.—Clover anthracnose (*Colletotrichum trifolii*), causes serious injury to red clover in certain regions. Bain and Essary (1906) issued a preliminary report on isolating an anthracnose resistant red clover. Healthy plants in a badly infested field were located late in the season after most plants had been killed by the disease. The seeds of the chosen plants were planted separately in alternate rows with ordinary commercial seed. Measures were taken to insure the infection of every seedling with anthracnose. By June 1 the commercial plants began to show symptoms of the disease and by the middle of September not more than 5 per cent. of them were living, while 95 per cent. of the selections were healthy and making a fair average growth. Some of the latter showed small lesions, but growth was not seriously injured.

ALFALFA

Alfalfa is one of the oldest, if not the oldest, plant cultivated for its forage only (Piper, 1916). Most of the cultivated forms

belong to the species *Medicago sativa*. The only closely related species of economic value is *M. falcata*, sometimes called sickle alfalfa or yellow-flowered alfalfa. The two species cross readily, as Waldron (1919) has shown (for pollination studies on alfalfa see Chapter III. Piper *et al* (1914) found that alfalfa set more seed when cross-pollinated than when selfed, although the selfed set considerable seed. It also was demonstrated that automatic tripping with consequent self-pollination may occur under certain conditions.

Grimm Alfalfa and Winter Hardiness.—Westgate (1910) and later Brand (1911) suggest that the origin of Grimm alfalfa is probably the result of natural crossing between cultivated alfalfa, *M. sativa*, and wild plants of the yellow-flowered sickle lucern, *M. falcata*, found especially in Germany, Austria, Roumania, and certain regions of Italy. The seed from which the Grimm variety eventually resulted was brought to Carver County, Minnesota, by a German immigrant farmer, Wendelin Grimm, in 1857. Here for 50 years the original variety was subjected to the severe Minnesota winters and as a result the non-hardy types were eliminated. At the present time Grimm alfalfa is probably the hardiest variety grown.

Waldron (1912) reported the result of testing for winter hardiness sixty-eight different strains of alfalfa assembled from various parts of the world. The trial was made at Dickinson, N. Dak. during the severe winter of 1908-09. The two strains of Grimm alfalfa included in the experiment proved to be the hardiest. On an average, less than 5 per cent. of the Grimm plants were killed and only one other strain showed less than 10 per cent. killed. Disregarding twelve strains which were destroyed completely, the average percentage killed for the other strains, considered as a unit, was 77.5.

To bring out the fact that differences between strains in their respective reactions to cold are genetic, Waldron computed

FIG. 52.—Structure of alfalfa flowers.

1. Branch showing flowers in position.
2. Single flower showing—*a*, standard; *b*, sexual column in contact with standard; *c*, keel; *d*, wings.
3. Seed pod.
4. Flower parts in position—*a*, undeveloped pod; *b*, ovary; *c*, filament; *d*, anther.
5. Same with all anthers removed except one to show stigma.
6. Anther.

Size: 1, about $\frac{1}{2}n$; 2, about $2n$; 3, about $\frac{1}{2}n$; 4, 5, 6, greatly enlarged.

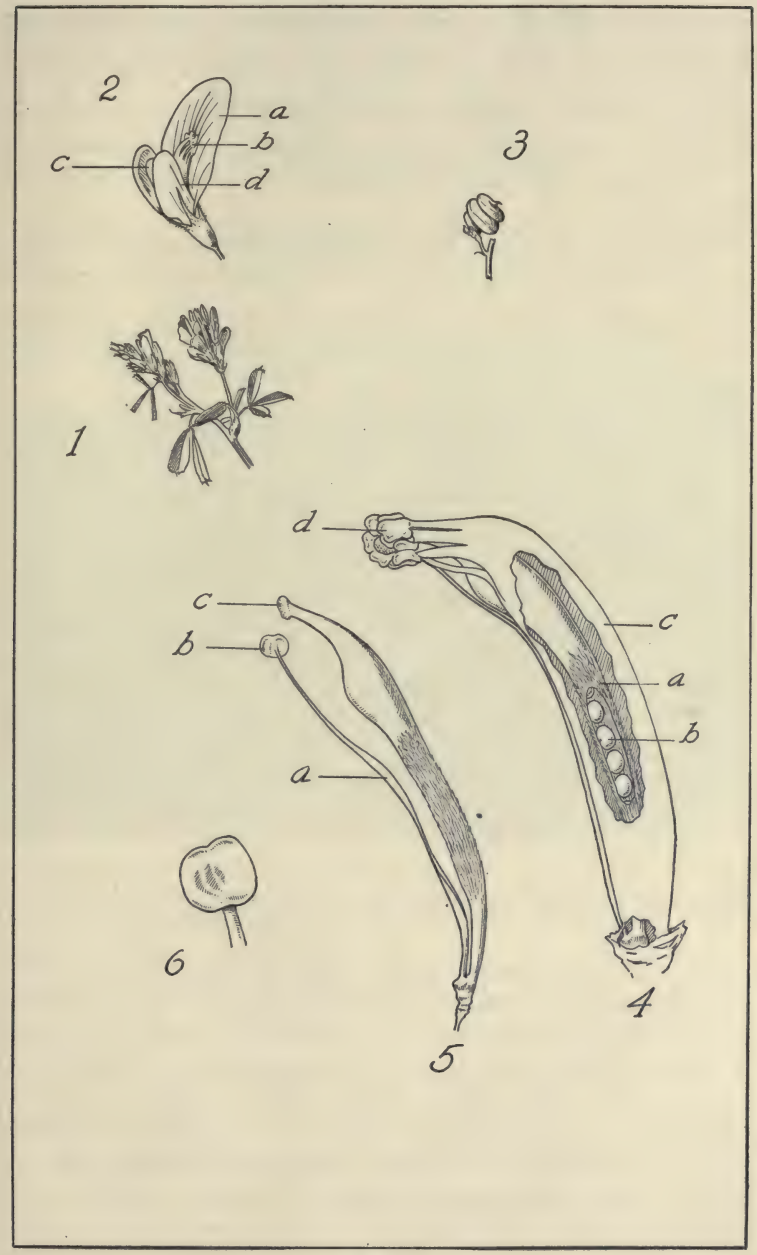


FIG. 52.

correlation coefficients. Two nurseries had been planted on succeeding years with the same strains taken from the same original lot of seed. The percentage of killing of the various strains in one nursery during the winter of 1908–09 was correlated with similar data collected from the other nursery after the winter of 1910–11. A correlation coefficient of $+0.62 \pm 0.06$ was obtained.

Some of the surviving plants of the different alfalfa strains were selfed and the seeds so obtained were planted separately in



FIG. 53.—Comparative hardiness of Grimm and common alfalfas. The two rows in the center are from Grimm seed. At either side are rows grown from southern grown common seed. 1916 season. (*Photo loaned by Arny.*)

a third nursery. Percentage of winter killing of these strains was taken and the correlation coefficient between the percentage of winter killing of the parental stock and that of the new strains was determined. The correlation coefficient obtained was $+0.46 \pm 0.07$. The mean winter killing (expressed in percentage) of the parental stock was 27.43 ± 1.75 as compared with 6.43 ± 0.66 for the strains coming from selfed seed. In other words, progress has been made toward isolating hardy biotypes.

CHAPTER XVI

POTATO IMPROVEMENT

Potatoes have been generally introduced into cultivation since the discovery of America, and are now a crop of major importance in many countries. The large number of varieties is an illustration of the rapid development in domestic plants of varieties which are suited to special soil and climatic conditions. As potatoes are reproduced commercially by tubers, they furnish an excellent illustration of the way in which vegetative reproduction modifies breeding methods.

Origin and Species.—There are from five to 100 species of tuber-bearing potatoes according to the number of forms which are recognized as separate species (East, 1908*b*: Wight, 1916). Whether the cultivated potato arose from a single wild species or from several is a debatable question. The preponderance of opinion is that there is only a single wild species, *Solanum tuberosum L.*, which deserves to be considered as the stem form from which all cultivated varieties arose. Wight (1916), after carefully examining herbarium material, previous records, and wild species, makes the following statements:

"Every reported occurrence of wild *S. tuberosum* that I have been able to trace to a specimen, either living or preserved in the herbarium, has proved to be a different species. I have not found in any of the principal European collections a single specimen of *Solanum tuberosum* collected in an undoubted wild state."

Berthault (1911) cites Heckel, Planchon, and Labérgerie as examples of recent workers who believe that other wild species gave cultivated *S. tuberosum* forms by mutation; Planchon believing that the original form was *S. commersonii*; Heckel that *S. maglia* through mutation produced cultivated potatoes; while Labergerie believed both of these species gave cultivated forms through mutation. Berthault attempted to answer the question by growing seeds and tubers of both these species and also by growing seed of several cultivated varieties. Progeny of seed or tubers of *S. maglia* and *S. commersonii* gave no forms which

approached in calyx or corolla characters the conditions found in *S. tuberosum* cultivated varieties. Progeny of seed of cultivated varieties showed Mendelian segregation, but no characters were obtained which had not been observed in ancient cultivated varieties. Wittmack (1909), after a careful botanical study of species, reached the conclusion that *S. tuberosum* was the stem species from which all cultivated potatoes arose.

The evidence presented by De Candolle (1886) seems sufficient to prove that the potato was wild in Chile and in a form which is very similar to that of our cultivated plants. Heckel (1912) reports a study of changes under cultivation of *Solanum tuberosum* forms collected in the wild in Bolivia and Peru by M. Verne. The wild plants were 0.25 meter in height, bore blue flowers and deep green foliage and tubers about the size of a hazel nut each produced at the end of a long stolon. These tubers were planted at Marseilles in a garden heavily fertilized with manure. Little change was observed in flower and fruit characters but there were pronounced changes in the subterranean parts. The yellowish tubers, each borne at the end of a much shortened stolon, contained a much greater amount of starch than wild tubers, while the characteristic bitter taste of the wild tubers disappeared. Much more profound changes occurred under cultivation with tubers of *S. maglia* (Heckel, 1909).

There seems to be no good reason for speaking of all these tuber changes as mutations. It seems more in line with modern genetic usage to consider them as the normal expressions of the inherited factors under the new conditions of environment which occur under cultivation.

The cultivated potato was first introduced into Spain and Portugal by the Spaniards during the first half of the sixteenth century.[1] Clusius described and illustrated the potato from plants sent him in 1588 by the governor of Mons. The published description was made in Clusius' "Rariorum Plantarum Historia" which appeared in 1601. The original plant obtained by Clusius bore two tubers and a fruit ball. This variety bore reddish tubers and light purple flowers. The spread from this introduction was probably next into Italy and from there early in the seventeenth century to Austria, then to Germany, from Germany to Switzerland and then to France.

Drake, after a West India piratical trip, took back the Roanoke

[1] East, 1908*b*.

colony to England, including Thomas Herriott. Probably potatoes were part of the stores obtained in the West Indies by Drake and these Herriott introduced into Ireland about 1586. This was the second introduction into Europe, the Spaniards deserving the credit for the first introduction. It is not known from what source the English colonists of Virginia and Carolina first obtained the potato, but it is generally believed to have been from Spanish or other travelers. Gerard described and illustrated the potato in his "Herbal" in 1597. The variety he described possessed light brown to yellowish tubers and violet to almost white flowers.

Inheritance.[1]—The transmission of potato characters through the seed is in conformity with Mendelian principles. Vegetative propagation allows the breeder to perpetuate any desirable genotype even though heterozygous, which is the usual condition in the potato plant. While, in general, self-fertilization of a commercial variety gives rise to seedlings which vary a great deal, it is comparatively easy to obtain homozygosity for some characters.

Tuber shape and size are important characters which are used as one means of varietal classification. Tuber shape has been found to depend essentially on the presence or absence of a single factor for length. According to this hypothesis a tuber may be homozygous long, homozygous round, or heterozygous long. Heterozygous long is the most variable of the three conditions. In one experiment two varieties with round tubers when selfed produced nothing but round tubers, while twelve varieties with oval tubers, when selfed, produced long, oval, and round tubered progeny. Nilsson (1912-13) found one variety of potato that did not breed true for round tubers. Long tubers were dominant to round in Fruwirth's (1912) experiments.

Depth of eye is a character of considerable economic importance. In general, shallow eyes were found to be dominant over deep eyes.

Several factors, in addition to a chromogen body, have been recognized in tuber coloration. Red potatoes contain two genes, *R*, a reddening factor, and *D*, a developer of pigment. Purple and black tubers have, in addition to *R* and *D*, another factor,

[1] The following discussion is based on inheritance studies made by Salaman (1909–11, 1910–11, 1911, 1912–13) and East (1910*b*) except where otherwise noted.

P. Segregating ratios were in accordance with the above factorial hypotheses. Wilson (1916) obtained only white tubers from selfed white-tubered varieties. Similar results have been obtained by other plant breeders which show that white is a recessive character. A certain amount of coloring in the young sprouts or shoots, stems, and sometimes in the leaf petioles was found associated with the presence of color in the tubers. With regard to flower color, three white-flowered varieties, selfed, produced only white flowers; and three out of four colored varieties, when selfed, produced both colored and white forms. Color is, therefore, dominant to its absence. Inheritance of this character may be explained by assuming the presence of a chromogen body and modifying factors. Heliotrope flowers are due to the chromogen body plus a reddening factor; purple flowers are produced by the addition of a purpling factor; white flowers may be due to the absence of one or more of these factors. Fruwirth (1912) found red tubers dominant over white, yellow flesh over white, and lilac-colored flowers over white. It was also found that different gradations of color were inherited.

Nilsson (1912–13) found a complicated flower color inheritance. A variety with violet-blue flowers gave, on selfing, progeny with red, violet-blue, near-red, purple, dark and light blue, and white flowers. A variety with light blue flowers, on selfing, yielded progeny showing simple monohybrid segregation with white recessive. Evidence that several factors were operating in the inheritance of tuber flesh color was also obtained. Some of the varieties with yellow flesh (tubers) bred true when selfed, others segregated as dihybrids with white recessive.

The inheritance of habit of growth was also studied. Plants may be upright, bushy, or procumbent. Bushy plants are heterozygous for habit of growth and many of them exhibit a distinct tendency to become procumbent. Homozygous forms of upright and sprawling plants may be isolated easily. Period of maturity is used as a means of varietal classification. It is probably inherited in the same manner as with other crops.

Sterility of the anthers has been found to be a dominant character. At first Salaman believed that its inheritance was due to a single differential factor but later evidence indicated a more complex manner of transmission. Plants producing pale heliotrope flowers were found to be heterozygous for pollen sterility.

MacDougal (1917) crossed the wild potato of Arizona, *S.*

fendleri, which grows at a high altitude and endures extremes of climate, with a domestic variety. The wild form produces small tubers. In the F_2 generation forms appeared which were identical with the wild parent together with many intermediate types.

Most of the observed variations in cultivated varieties have occurred in the tubers, although the English ash-leaf varieties are examples of a variation in leaf shape (East, 1907*b*).

Production of New Forms.—For the purpose of differentiating between two important phases of potato improvement, Stuart (1915) has referred to "selection" as the "isolation and asexual propagation of desirable strains or types" while "breeding" is used only for sexual reproduction. With certain crops, such as the potato, this terminology is distinctive. Such a restricted usage of the word "selection" seems undesirable from the plant-breeding standpoint. The same idea can be obtained by the use of "clonal selection" to refer to the asexual propagation of desirable strains or types.

Systematic plant breeding with the idea of combining the desirable characteristics of two parental varieties can be carried out only after the breeder has familiarized himself with the characters of particular varieties and of their wild relatives. Thus, with the potato as with other crops the breeder should first determine the ideal toward which he will work. Parental varieties should than be selected because of some desirable characters. By recombination of the favorable characters of both parents, improvement may be obtained. Gilbert (1917) has listed certain characters of the potato which are universally desired. Some of these are:

1. High yield.
2. Good quality.
3. Disease-resisting capabilities.
4. Good keeping quality.
5. Good color of flesh and skin.
6. Skin of desirable texture.
7. Tubers of good shape.
8. Shallow eyes relatively few in number.
9. Upright, vigorous plants.
10. No tendency to make second growth.

The desirability of most of these characters is self-evident. The chief difficulties in the way of developing a standardized method of attack arise from:

1. The heterozygous condition of most varieties.
2. The difficulties of obtaining crossed seed.

The heterozygous condition need not be further emphasized. Conditions are much the same as in the fruit crops.

The Difficulties of Obtaining Crossed Seed.—The technic of making a cross is very simple. According to East (1908*a*), "The flowers close slightly about dusk and open in the morning between five and six o'clock. The pollen appears to be in the best condition for use on the second day of blooming." Stuart (1915) collects flowers to be used as the male parent in small sacks. After the pistil is removed from these flowers the anthers are tapped sharply with a pair of forceps, the pollen is collected

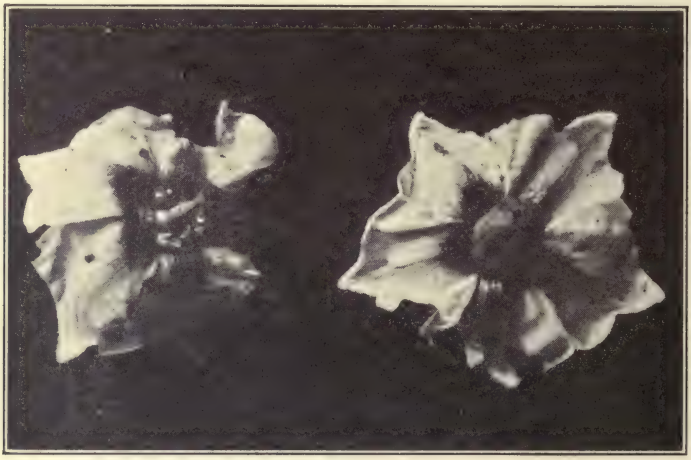


FIG. 54.—Emasculated and unemasculated potato blossoms. (*After Stuart.*)

on the thumb nail and then applied to the pistil of the emasculated flower. The flowers are receptive two to four days after emasculation. East (1908*a*) stated the belief that the potato is usually self-fertilized. He also observed the fact that insects were seldom seen to visit the flower. Salaman (1910–11) believes it unnecessary to cover the flower before or after pollination. Stuart, however, used 1-lb. bags and found that if a certain amount of foliage was included in the bag the use of bags did not cause a lowering of the number of seeds set. An average of between one and two hundred seeds was obtained from each successful cross by Stuart.

The chief difficulty is that many varieties do not bloom very

freely, although the general belief is that all varieties may bloom under certain conditions of environment. East (1908*a*) classified varieties as follows:

"1. Varieties whose buds drop off without opening.

"2. Varieties in which a few flowers open, but which immediately fall.

"3. Varieties whose flowers persist several days, but which rarely produce viable pollen.

"4. Varieties which under most conditions always produce viable pollen."

In 487 out of 721 varieties under observation the buds fell off before the flowers opened. Stuart, however, obtained a much higher percentage of varieties which produced flowers in which the blossoms opened before the buds fell. These results are given to emphasize the fact that conditions widely influence seed production.

The lack of fertile or healthy pollen in many varieties prohibits their use as parents. The relation between the percentage of healthy pollen and fruit production was determined by East (1908*a*) for a considerable number of crosses (see Table LIV).

TABLE LIV.—RELATION BETWEEN PERCENTAGE OF VIABLE POLLEN AND FRUIT PRODUCTION

Viability	Fruit production				
	None	Difficult	Medium difficult	Medium	Good
0– 25 per cent. healthy.....	20				
26– 50 per cent. healthy.....	5	5	1		
51– 75 per cent. healthy.....	..	2	3	3	2
76–100 per cent. healthy.....	..	..	..	6	3

Somewhat similar results were obtained showing a positive correlation between fruit production and the percentage of multinucleate pollen grains. Such grains may be determined under the microscope by their slight protuberances. Germination tests in seven per cent. sugar solution showed that a pollen tube grew from each protuberance in a multinucleate grain. These results obtained by East have been corroborated by the studies of Stuart. In some cases, however, seed production is not difficult to obtain as the data from Stuart show (Table LV).

TABLE LV.—RESULTS OF POTATO CROSSES MADE ON THE POTOMAC FLATS, WASHINGTON, D. C. IN 1910

Parentage of cross	Date emasculated	Date pollinated	Number of flowers crossed	Number of seed balls formed	Number of seeds	Percentage of seeds germinated
Irish Cobbler × Irish Seedling.	July 28	July 30	6	6	964	80.0
Irish Cobbler × Irish Seedling.	July 28	July 30	7	5	984	83.5
Eureka × Keeper.....	July 28	July 30	7	5	1,154	78.3

Improvement Through Seedling Production.—Probably no statement could be more illuminating than Stuart's discussion regarding early studies of potato improvement in the United States. The facts here related are taken from Stuart's publication.

During the period from 1840 to 1847 the wide occurrence of potato blight focussed the attention of potato growers upon the need of more resistant varieties. Rev. C. E. Goodrich, of Utica, N. Y., believed this susceptibility to diseases was a result of long-continued asexual propagation. Through the agency of the American consul at Panama, South American varieties were introduced. Goodrich grew seedlings from Rough Purple Chili, one of the introduced varieties, and obtained a new variety which he named Garnet Chili. This new variety was introduced into the trade in 1857. Between 1849 and 1856 Goodrich raised a total of 8,400 seedlings. These experiments had considerable effect on the work of other breeders. In 1861 Albert Bresee, of Hubbardton, Vt., grew a naturally fertilized seed ball produced by Garnet Chili. One of the seedlings produced was distributed under the name of Early Rose. The most careful breeder of this period was C. C. Pringle, of Charlotte, Vt. He selected varieties for crossing because of desirable characters. A variety by the name of Snowflake was one of the best known of his productions. Pringle, in the early seventies, contracted to produce potato seed for $1,000 a pound.

Numerous varieties, probably resulting from naturally pollinated seed, were introduced by E. S. Brownell, of Essex Center, Vt. Among the better known of these were Brownell's Best, Beauty, Eureka, and Winner. Among other well-known varieties which were introduced about this time was the early maturing variety, Early Ohio. Alfred Reese produced this variety, which

was introduced in 1875, from a seedling of Early Rose. One of the first plant productions of note of that celebrated breeder, Luther Burbank, was obtained by growing seedlings of a potato ball which he found on an Early Rose vine in his mother's garden at Lancaster, Mass. Of 23 seedlings grown, one was of much promise. This was introduced by Gregory in 1872 as Burbank's Seedling. From naturally fertilized seed of Garnet Chili,



FIG. 55.—An extra-promising first-year seedling. Crop of 1910. 24 tubers. (*After Stuart.*)

E. L. Coy of West Hebron, N. Y., obtained a variety that was introduced in 1878 as Beauty of Hebron. These early experiments which produced some varieties that are still grown illustrate the marked effect which the introduction of a single variety may have on the production of new forms. Some of the varieties which resulted from the introduction and breeding experiments of Rev. C. E. Goodrich are here listed:

TABLE LVI.—PEDIGREES OF SOME POTATO VARIETIES

Breeder	Variety used for seed	Seedlings named
Rev. C. E. Goodrich	Rough Purple Chili	Garnet Chili
Albert Bresee	Garnet Chili	Early Rose
Alfred Reese	Early Rose	Early Ohio
Luther Burbank	Early Rose	Burbank
E. L. Coy	Garnet Chili	Beauty of Hebron

These early studies illustrate the general mode of production of new potato varieties. Certain methods are of value in giving the seedlings a good start. In the latitude of Washington, Stuart recommends sowing the seed in the greenhouse early in March and transplanting the seedlings from 3-in. pots into the field in May. The plants are placed in rows 3 ft. apart and spaced at a distance of 2 ft. apart in the row. Results indicate that seedlings producing tubers of irregular shape or those with deep red or purple skin may well be discarded after the first year's trial. After another year's study those strains with undesirable characters such as low yielding ability, undesirable shape, deep eyes, unusual susceptibility to fungous diseases and



FIG. 56.—An unpromising first-year seedling. Crop of 1910. Note the large number of small, irregular shaped tubers. (*After Stuart.*)

straggling or weak vine growth, should be discarded and the few more promising types given a wide test to determine their adaptability and value under different conditions.

Clonal Selection.—The subject of bud mutations in potatoes is a somewhat difficult one, for there are numerous reported cases of such sudden changes. Many of the experiments were not performed with sufficient care to furnish acceptable evidence, although numerous apparently authentic cases of color changes have been reported. As an illustration of carefully controlled experiments those carried on by East (1910*a*) may be cited. In these studies each variety worked with was started from a single hill. During the course of the study, five permanent changes

from pink to white tubers, two permanent changes from long to round tubers, and four instances of changes from shallow to deep eyes were observed. On the basis of the modes of inheritance of these characters, the hypothesis was made that the changes resulted from the loss of dominant factors. Experiments in selection for high nitrogen content gave negative results. The statement was made, "it is true that all of the asexual variations have been losses of characters, while in sexual reproduction the formation of new characters occurs." This certainly substantiates the belief that the production of improved varieties of potatoes through bud mutation is not a promising method of attack. East quotes A. W. Sutton, who states:

"I have no hesitation in affirming that there is no potato in commerce in England, and I might say in Europe, which owes its origin as a distinct potato to bud variation in any form whatever."

If this statement is true, it seems fair to conclude that there has been a somewhat loose usage of the term "bud mutation" in its application to raising the standard of a variety by any of the well-known methods such as tuber unit or hill selection (see Chapter XVIII). Accumulated evidence certainly points to the belief that the chief value of such work rests on the probable elimination of degenerate strains. Evidence from Canada presented by Macoun (1918) is particularly illuminating. Four varieties, Early Rose, State of Maine, Empire State, and Delaware, were grown in Canada at the Experimental Farm at Ottawa from 1890 to 1909 inclusive. The better tubers were selected from each year's crop and used to plant the following crop. Results are presented in Table LVII.

TABLE LVII.—AVERAGE YIELD OF POTATOES OVER THE FIRST FOUR AND LAST FOUR YEARS OF A 16-YEAR PERIOD AND SUBSEQUENT YEARLY YIELDS OVER A FOUR-YEAR PERIOD

Variety	Year					
	1890–1893, bu.	1902–1905, bu.	1906, bu.	1907, bu.	1908, bu.	1909, bu.
Early Rose.....	257	317	150	128	69	18
State of Maine....	325	361	132	174	97	62
Empire State.....	301	338	132	117	117	62
Delaware.....	296	352	103	114	156	53
Average.....	295	342	129	133	110	49

For the 16-year period from 1890 to 1905, inclusive, the varieties were kept in a high state of productivity "due, no doubt, to careful selection and good cultivation each year." In 1906, however, there was a marked falling off in yield due to the unfavorable season. In the early part of the season there was sufficient rain but at about the time of the last cultivation, hot dry weather set in and continued throughout the season. During July there was also a severe attack by aphis. The vines, therefore, presented a stunted appearance and dried up early in the fall, the yield of tubers being very low. In 1907 and 1908 the seasons were also very unfavorable. The best tubers were again planted in 1909 and although the tubers used for planting presented a very favorable appearance, the yields were very low. A comparison was made in 1909 of tubers grown continuously at the Central Experiment Farm and newly imported tubers grown under more favorable conditions. The yielding ability of the imported tubers exceeded that of the Central Farm tubers by as high as 500 per cent. in some cases.

The plant breeder is naturally interested in the subject of whether these are instances of bud variations due to unfavorable environment. If so, they should be permanent changes. If, on the other hand, they are non-heritable variations, this does not affect the practical importance of tuber selection as a means of obtaining high yields. Macoun (1918) has furnished evidence which helps to clarify our ideas on this question. From time to time tubers were sent from Ottawa to the branch stations, on the prairies, where potatoes usually grow very vigorously. In 1916 the following question was asked:

"You will, no doubt, remember that potatoes sent you from Ottawa are usually weak growers when you receive them. I would be glad if you would inform me for how many seasons that weak growth continues, or do they make a strong growth the next year, the same as the ones you have been growing for several years?"

Answers made by the superintendents of these prairie farms showed that the first year's crop from tubers sent from the Central Farm was very small. From one to three years elapsed before varieties introduced from the Central Experimental Farm yielded as well on the prairies as those varieties which had been continually grown on the prairies.

Much of the so-called "running out" or degeneracy in pota-

toes has been traced to certain plant diseases (Stewart, 1916; Orton, 1914) which have been variously named as leaf roll, mosaic, and curly dwarf. Quanjer (1920) has presented evidence to show that these three diseases may be stages of the same disease, which is transmissible from plant to plant. Similar results have been obtained at University Farm.[1] The disease is called "mosaic dwarf" by Krantz and Bisby in unpublished investigations. That rejuvenation of a variety is possible through its introduction and growth under a more favorable environment is illustrated by studies which have been carried on



FIG. 57.—Progeny of single tubers as grown at University Farm, 1918. Some tubers give vigorous progeny, others produce only small, weak, degenerate plants. (*Courtesy of Krantz.*)

coöperatively between the Division of Horticulture of the Minnesota Central Station and the sub-stations. Yields for Minnesota No. 2 at University Farm for 1914, 1915 and 1916, respectively, were 196, 169 and 22 bu. This shows the rapid reduction in yield which is obtained by the continued use of tubers saved at University Farm. Tubers of Minnesota No. 2 saved from the 1916 University Farm plot gave a yield of 170 bu. at Duluth in 1917. Tubers from this Duluth plot yielded 300 bu. at Grand Rapids in 1918. Whether a badly diseased

[1] Data on running out and on field experiments in Minnesota were furnished by F. A. KRANTZ of the Division of Horticulture, Minnesota Experiment Station.

variety can be rejuvenated by planting under a favorable environment tubers from diseased plants is as yet an unanswered question.

The rapid deterioration of varieties when University Farm tubers are used for their propagation is believed to result from these transmissible diseases which are now called "mosaic dwarf." Degeneracy can apparently be prevented by covering that part of the field in which tubers are to be saved for the next year's planting by a cheese-cloth cover. The following data with the variety Green Mountain seem sufficient authority for this statement:

TABLE LVIII.—DEGENERACY PREVENTED BY USING TUBERS OF VINES WHICH WERE COVERED WITH A CHEESE CLOTH COVER

Source of timber used	Year grown	Yield per acre, bu.	Probable error in per cent.
Grown in open at University Farm, 1917....	1918	172	4.6
Grown under cheese-cloth cover at University Farm, 1917.....	1918	223	5.4
Newly introduced stock.....	1918	205	1.7
Grown in open at University Farm, 1917 and 1918.....	1919	1.5	
Grown under cheese-cloth cover at University Farm, 1917 and 1918.....	1919	285	4.8
Newly introduced stock.....	1919	272	1.5

All seed stock was obtained from the same grower at the North Central Experiment Station, Grand Rapids, Minn. Whether all degeneracy is due to such transmissible diseases is as yet unanswered. Possibly unfavorable cultural conditions may also affect the development of the tuber so that the yield of the following year's crop may be modified.

Another explanation of degeneracy has been commonly mentioned. This is the hypothesis that continued asexual propagation causes senility or degeneracy. Perhaps this question may be answered for the potato by the consideration of a fact reported by Heribert Nilsson (1913). In a report of yields of 67 varieties, as tested in Sweden, he emphasized the fact that a variety "Hvit Jämtlandspotatis" which has been cultivated more than 100 years proved to be the highest yielder. This is given as a refutation of the theory of senility.

It has not been the intention in this discussion to lead the

practical breeder to discard "clonal selection" as one means of obtaining high yields, for it is a recognized fact that seed plot methods are of much practical importance. The results, however, are probably not due to the isolation of bud mutations but rather to the use of tubers which have developed normally and which furnish the right conditions to give the resultant plants a favorable start. May not the conditions be much the same as with any vegetatively propagated plant. Bonnier, for example, found that about three years are required before a low-

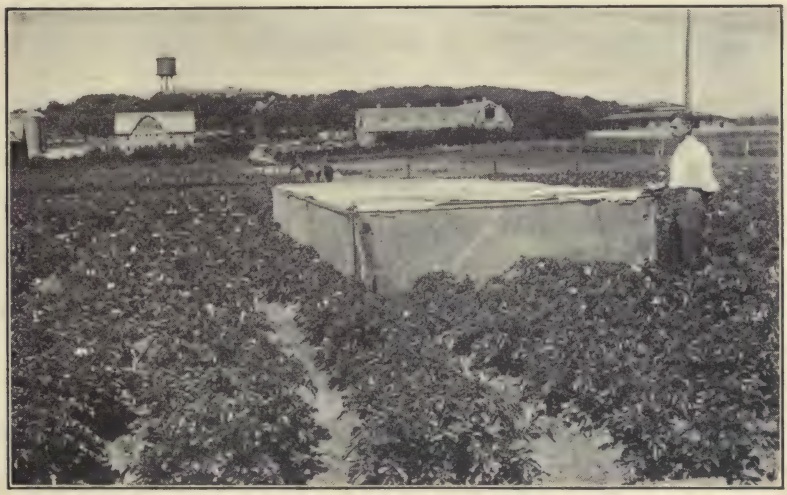


FIG. 58.—Tubers produced under such a cheesecloth cover have given good yields during the seasons 1918 and 1919 while tubers from uncovered vines produced very inferior yields. University Farm, St. Paul, Minnesota. (*Courtesy of Krantz.*)

land dandelion transported to alpine conditions fully expresses the characters of a dandelion plant which had been grown under these conditions for many years. On returning the same plant to the lowlands about the same number of years elapsed before the plant had again fully attained the lowland habit. This is probably not a germinal change but the normal expression of the plant under a particular environment. With the clonally propagated potato there is a cumulative response to unfavorable conditions. Such conditions modify the plant's development and therefore influence the development of the following year's crop. There seems no reason for believing that an actual germinal mutation has occurred.

CHAPTER XVII

BREEDING OF VEGETABLES

SELF-FERTILIZED VEGETABLES

The long periods of cultivation and the various environments to which many of our vegetables have been subjected, have served to increase the number of varieties. Most of the vegetable varieties have been produced by commercial seed firms or by seed growers. An examination of any seed catalog shows numerous new forms which are being constantly introduced into cultivation. There has been a marked tendency among seedsmen to give new trade names to old standard varieties. This has led to a great deal of confusion in nomenclature and much difficulty has been experienced in varietal identification. There is need of a more scientific test of varieties prior to introduction and of a standardization of varieties. Considerable progress has been made in classification of some vegetables. More information is needed regarding the mode of pollination and inheritance of special characters before methods of breeding can be intelligently applied. In this chapter the origin of both cross- and self-fertilized vegetables is briefly summarized. The mode of inheritance of special characters of the self-fertilized vegetable species, pea, bean, tomato, and pepper are given, together with a brief discussion of methods of breeding.

Origin of Vegetables.[1]—The ancient Greeks and Romans were familiar with some of our garden vegetables; on the other hand, many are of more recent origin and new varieties are being constantly introduced. The discovery of America introduced to civilization such important vegetables as the Irish potato,

[1] For a complete history of the origin of vegetables see De Candolle, A., Origin of Cultivated Plants, Kegan Paul, Trench & Co., London, Second Edition, 468 pages, 1886; Henslow, G., The Origin and History ofOur Garden Vegetables and Their Dietetic Values, in *Jour.* Roy. Hort. Soc., vols. 36 and 37, 1910–11 and 1911–12; Sturtevant, E. L., History of Garden Vegetables, in *Am. Nat.*, vols. 23, 24, and 25, 1889, 1890, and 1891.

sweet corn, tomato, bean, sweet potato, pumpkin, squash, and pepper. Nearly all the other cultivated vegetables of temperate climates are indigenous to Europe or Asia.

Sweet corn, which is one of the most highly prized foods grown in America, is probably of recent origin. In Bailey's (1900) Cyclopedia of American Agriculture, Volume 2, page 402, the following statement occurs:

"The first sweet corn cultivated in America was derived from the Susquehanna Indians in 1779 by Captain Richard Begnall, who accompanied General Sullivan on his expedition to subdue the Six Nations."

How long *Zea mays saccharata* had been under cultivation is

TABLE LIX.—ORIGIN AND ANTIQUITY OF SOME VEGETABLES

Vegetable	Botanical name	Probable origin	Years cultivated
Asparagus	Asparagus officinalis	Europe, west temperate Asia.	*B*
Bean, lima	Phaseolus lunatus	Brazil.	*E*
Bean, common	P. vulgaris	S. Am. found in Peruvian tombs.	*E* (?)
Beet	Beta vulgaris	Canaries, Mediterranean basin, western temperate Asia.	*B*
	Tops as food		
	Roots as food	A result of cultivation.	*B*
Cabbage	Brassica oleracea	Europe	*A*
Carrot	Daucus carota	Europe, west temperate Asia (?).	*B*
Celery	Apium graveolens	Temperate and southern Europe, northern Africa, western Asia.	*B*
Corn, sweet	Zea mays var. saccharata		
Cucumber	Cucumis sativus	India.	*A*
Lettuce	Lactuca sativa	Southern Europe, northern Africa, western Asia.	*B*
Muskmelon	Cucumis melo	India, Beluchistan, Guinea	*C*
Onion	Allium cepa	Persia, Afghanistan, Beluchistan, Palestine (?)	*A*
Parsnip	Pastinaca sativa	Central and southern Europe.	*C*
Pea, garden	Pisum sativum	From the south of the Caucasus to Persia (?), northern India (?).	*B*
Pepper	Capsicum annuum	Brazil (?)	*E*
Pumpkin	Cucurbita pepo	Temperate North America.	*E*
Radish	Raphanus sativus	Temperate Asia.	*B*
Salsify	Tragopogon porrifolium	Southeast of Europe, Algeria.	*C* (?)
Spinach	Spinacia oleracea	Persia (?).	*C*
Sweet potato	Convolvulus batatas	Tropical America (where?).	*D*
Tomato	Lycopersicum esculentum	Peru.	*E*
Turnip	Brassica rapa	Europe, western Siberia (?)	*A*
Watermelon	Citrullus vulgaris	Tropical Africa.	*A*

A = Species cultivated more than 4,000 years.
B = Species cultivated more than 2,000 years.
C = Species cultivated less than 2,000 years.
American species:
D = Cultivation ancient in America.
E = Cultivation before discovery of America, but not showing signs of great antiquity.

not known, but there is considerable evidence to substantiate the belief that at least the main types of corn, *Zea mays indentata* and *Zea mays indurata*, were cultivated a long time before the discovery of America.

Table LIX taken from De Candolle (1886) presents a summary of the origin of some common vegetables.

PEAS

Some Classification Characters.—Considerable historical interest attaches to the pea because of the fact that in studying the inheritance of certain characters in this plant Mendel discovered his now famous principles. Garden peas (*Pisum sativum*) are of two kinds, shelling and edible-pod. In the former, seeds only are used as food, while in the latter both pods and seeds may be so utilized. By far the greater part of the garden peas grown belong to the shelling group. Commercial varieties of garden peas are classified on the basis of habit of growth—climbing, half-dwarf, and dwarf; and length of time to mature—early, medium, and late. Peas of the early varieties may be round or wrinkled. Most of the medium and late maturing varieties belong to the sugar peas, which have wrinkled seeds when mature. Size of pod is another important classification character. Ripened pods may be inflated or somewhat constricted.

Inheritance.—In a reciprocal cross of the varieties Autocrat and Bountiful, it has been suggested (Keeble and Pellew, 1910) that the inheritance of the character tallness involved two factor differences, one for length of internode and one for thickness of stem. In certain crosses White (1918) finds the inheritance of stature still more complicated. Tall varieties (over 4.5 ft.) are divided into three groups and half-dwarfs are separated into two groups. The factorial scheme suggested is as follows:

FIG. 59.—Flower structure of pea.

1. A single flower—*a*, petals of calyx; *b*, side view of corolla.
2. Front view of fully open flower—*a*, petal of calyx; *b*, standard; *c*, wing; *d*, keel.
3. The sexual organs removed from the bud. (*Adapted from Muller.*) *a*, Filament; *b*, anther; *c*, style; *d*, stigma hairs.
4, 5. Anthers.
6. Cross section ovary.
9. Longitudinal section ovary.

Size: 1, $\frac{5}{4}n$; 2, $\frac{5}{6}n$; 3, greatly enlarged; 4, 5, $100n$; 6, greatly enlarged; 7, $8n$; 8, $40n$; 9, $40n$.

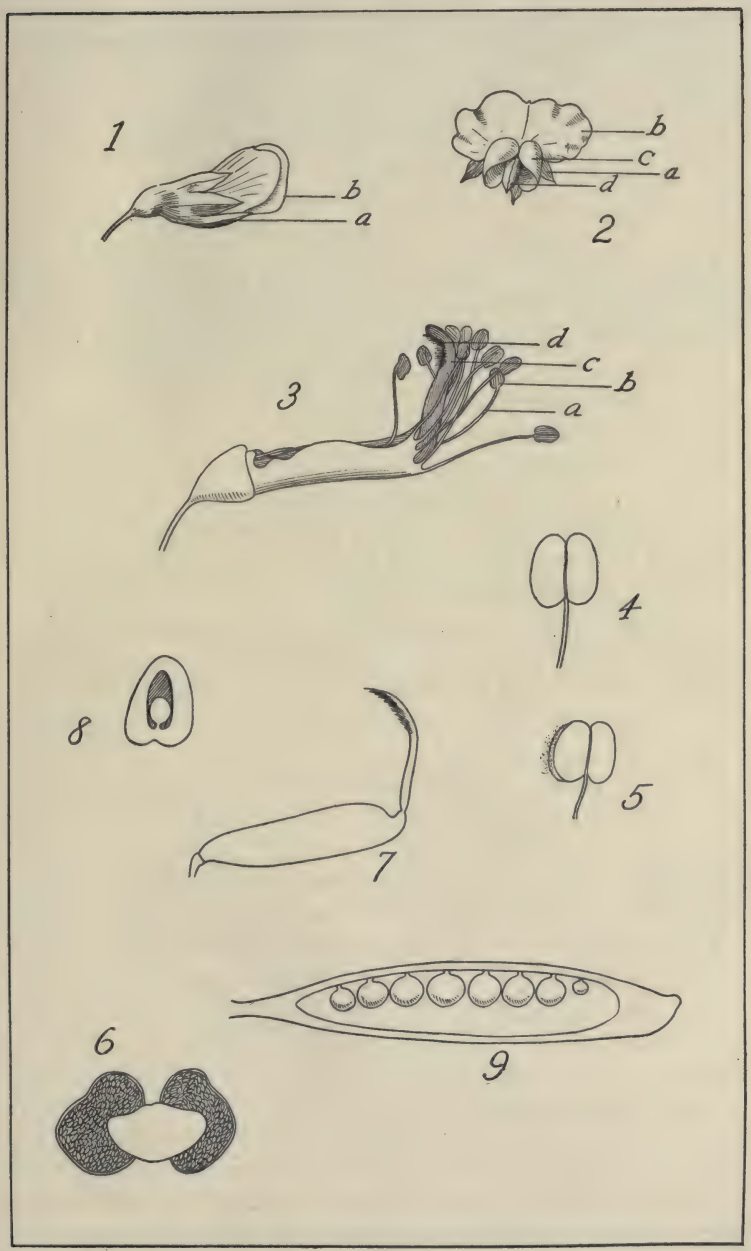


FIG. 59.

Length of internodes. . . { Le = long internodes; Le_1 = very long internodes

Number of internodes. . { T = 20–40 internodes; T_1 = 40–60 internodes; T_2 = 20–30 internodes

Absences

le = short internodes

t = 10–20 internodes

Le is the height factor isolated by Mendel, while *T* is Keeble and Pellew's factor for thickness of stems which White has interpreted as a factor for internode number and internode length. On the factorial basis given, the phenotypic condition of the talls—of which there are three classes—would be:

1. *Le T* = 20–40 long internodes.
2. *Le* T_1 = 40–60 long internodes.
3. Le_1T_2 = 20–30 very long internodes.

The phenotypic nature of the half dwarfs would be:

4. *Le t* = 10–20 long internodes.
5. *le T* = 20–40 short internodes.

True dwarfs would represent the absence of both dominant factors *Le* and *T* or *let*. With the same material that Mendel used, the same results for height have been obtained.

The inheritance of time of flowering involves several factors as is shown by complicated F_2 ratios (Tschermak, 1916) (Keeble and Pellew, 1910). Keeble and Pellew found linkage between the factors for thick stems and late maturity and likewise between the opposite condition, thin stems and early maturity.

Vilmorin (1910) made a large series of crosses with edible pod races. In some cases both F_1 and F_2 produced only plants with edible pods. In other crosses hard inedible pods were produced in F_1 and ratios of 9 hard to 7 edible were obtained in F_2. Results may be explained by the supposition that hard pod varieties (development of parchment-like tissue) may be due to the presence of two factors (White, 1917) *PPVV*. Non-parchment varieties may have either the formulæ *PPvv*, *ppVV* or *ppvv*. White cites earlier workers who have always found parchmented pods to be inflated and non-parchmented to be constricted. Nohara (1918), in a cross between a Japanese pea and a French variety, both of which produced soft edible pods, obtained a ratio of 9 parchmented to 7 non-parchmented in F_2. Results were also explained by a two-factor hypothesis.

Tschermak (1916) has compiled a brief summary of the mode of inheritance in the garden pea with particular reference to economic characters. Table LX is made up from his summary.

TABLE LX.—INHERITANCE IN THE GARDEN PEA

	Dominant	Recessive
Color of cotyledon[1]	Yellow	Green
Form of cotyledon[1]	Round	Wrinkled
Arrangement of seed in pod	Loose	Crowded close together
Character of pod	Full and smooth	Constricted and wrinkled
Ends of pod	Blunt	Pointed
Color of unripe pod	Green	Yellow
Character of inflorescence	Raceme	Umbel
Tendrils	Present	Absent
Leaf surface	Pubescent	Smooth
	Imperfect dominance	
Setting of pods per plant	Few	Many
Number of flowers in raceme	3–5	1–2

[1] Segregation apparent in seeds borne by F_1 plants.

All the characters listed above show, as a rule, simple monohybrid segregation in F_2. In addition to these the following characters are intermediate in F_1 and give complex ratios in F_2 according to Tschermak:

Long pods *vs.* short pods
Broad pods *vs.* narrow pods
Large seed *vs.* small seed.

White (1916) has done much to increase our knowledge of the genetic factors and their interrelations. Cotyledon colors were found to be explained satisfactorily by the following formulæ:

GGII = Dominant yellow varieties. (1)
ggii = Recessive yellow varieties. (2)
GGii = Green varieties. (3)

All peas have yellow pigment in the cotyledon. *G* is a factor for green pigment and *I* a factor which causes green pigment to fade on the maturity of the seed. "Goldkönig" was the only variety containing the genetic formula *ggii*.

Table LXI is a statement of the genetic factors of peas as determined by White (1917), who made a careful review of earlier studies and who has also studied a number of new crosses.

TABLE LXI.—LIST OF PISUM FACTORS, ALPHABETICALLY ARRANGED, AND THEIR CORRESPONDING CHARACTER EXPRESSIONS

No.	Factor	Expression
1	*A*	Salmon-pink or rose flower color. With *CD* gives reddish leaf axils.
2	*B*	Purpling factor plus *A* gives purple flowers. With *CD* plus *A* gives purplish leaf axils and stem bases.
3	(*Bl*)	Glaucous foliage, stems and pods (with *W*); "bloom."
4	(*Bt*)	Pods with blunt apex.
5	*C*[*A*]	With *D* gives leaf axil and stem color.
6	*D*	With *C* gives leaf axil and stem color.
7	*E*[*A*]	With *F* and *B* gives purple dotting on seed coats; in the absence of *B* gives reddish dots.
8	(*Ef*)	Modifies the expression of (*Lf*) toward earlier flowering.
9	*F*	With *E* and *B* gives purple dotting on seed coats; in the absence of *B* gives reddish dots.
10	(*Fa*)	Axillary flowers, round stems, regular phyllotaxy.
11	(*Fn*)	1 to 2 flowers per peduncle.
12	(*Gc*)[*A*]	Yellowish green to grayish brown seed-coat color (weak chromogen factor), brown hilum.
13	*G*	Green cotyledon pigment.
14	(G_p)	Green pod color.
15	*H*	Brightener or inhibitor of expression of (*Gc*.)
16	*I*	Factor which causes green cotyledon color to fade.
17	*J*	With (*Gc*) gives dark brown seed-coat color.
18	L_1[*A*]	With L_2 gives indent peas.
19	L_2	With L_1 (*A*) gives indent or dimpled peas.
20	(*Le*)	Long internodes; with *T* gives tall plants.
21	(*Lf*)	Primarily responsible for late flowering.
22	*M*	Brown or maple mottling on seed coat; or "ghost mottling" in absence of *A*.
23	*N*	Violet eye on seeds.
24	*O*	Green foliage, stems, and pods.
25	*P*	Inflated, parchmented, nonedible pods with *V*.
26	P_1	With P_2 gives purple pods.
27	P_2	With P_1 gives purple pods.
28	(*Pl*)	Black-eyed seed-coat pattern.
29	*R*	Round, smooth seeds with simple, oval starch grains, low water content and with excellent powers of germination under unfavorable weather conditions.
30	*S*	Pods with seeds separated or free.
31	*T*	Tall, robust plants, large number of internodes.
32	(*Tl*)	Leaves with tendrils.
33	*U*	Dark self-colored purple seed-coat.
34	*V*	With *P* gives parchmented, smooth pods.
35	*W*	With (*Bl*) gives glaucous foliage, pods.

The presence and absence of these thirty-five factors are genetically responsible for seventy or more differential characters. As is noted in the table, there is a modifying effect of one factor upon another in certain cases. Studies have also shown that certain environmental conditions may modify a particular inheritance in such a way that the true genetic nature can not be determined by inspection. This is an instance which should help to impress upon the student the necessity of the controlled breeding test as a

means of determining the genetic nature of any particular variety or strain.

Factors *A*, *C*, *E*, (*Gc*) and L_1 appear absolutely coupled and may, therefore, be considered to be a single factor with several separate expressions. This factor gives salmon-pink or rose color to the flower, and to the leaf axil, and to the stem in the presence of *D*; purple dotting on seed-coats in the presence of *F* and *B*, with reddish dots when *B* is absent and *F* is present; yellowish green to grayish brown seed-coat color, brown hilum; indent peas in the presence of L_2.

The results of examining many thousand F_2 generation progeny indicate that factors *A*, *B*, (*Fa*), *I*, (*Le*), *G*, and *R* are independently inherited.

Four groups of linked factors were found. These, according to the factorial notation used by White, are:

Group	Partially linked	Ratio of non-crossovers to crossovers
1	(*Bl*)*S*	8:1
2	*A*(*Lf*)	7:1
3	*R*(*Tl*)	63:1
4	*GO*	Undecided

BEANS

Some Classification Characters.—The species[1] of garden beans most commonly grown are *Phaseolus vulgaris* and *P. lunatus*. The former is divided, from the standpoint of use as food, into snap and shell beans, although there is some overlapping in these groups. Shell beans are sometimes used as snap beans and *vice versa*. Time required to mature, habit of growth, whether climbing or bush, and size of plant are characters always described by commercial seedsmen. Length of bearing period is also an important character. Commercial growers sometimes desire varieties which may be harvested in a few pickings but for the home and general gardener, a variety with a longer bearing period is usually preferred. Size and shape of pod, number of seeds per pod in the case of snap beans, quality and color of the pod, are used in classification; with snap beans, stringless, fleshy, fine-grained pods are most desirable. The ease with which dry

[1] For a discussion of the classification of garden beans and a description of varieties see Tracy, W. W., American Varieties of Garden Beans, U. S. D. A., B. P. I. *Bull.* 109, 173 pages, 1907; Jarvis, C. D., American Varieties of Beans, Cornell Agr. Exp. Sta. *Bull.* 260: 149–255: 1908.

shell beans may be thrashed is of economic importance. In this group, color, size, and shape of seeds are usually included in varietal descriptions. Both productivity and disease resistance may differ strikingly in different varieties of beans.

Inheritance.—Seed-coat color has been shown by Shaw and Norton (1918) to involve several factor differences. The work was carried on with twenty-one varieties including more than 40,000 plants. Crosses between mottled and self-colored varieties yielded mottled beans in F_1 and showed 3 : 1 ratios in F_2. Mottled × white varieties gave mottled in F_1, and in F_2 the ratio of 9 mottled to 3 self-colored to 4 white usually resulted. It was demonstrated that pigment patterns and pigment colors were controlled by distinct factors. All plants with white or eyed beans bore white flowers while plants with mottled or self-colored beans usually bore pink flowers.

The inheritance of stature in beans, as in peas, is in some crosses dependent on a single factor difference while in other crosses several factor differences are involved. Emerson (1916) has explained the result of crossing a tall pole (indeterminate growth) bean and a short bush (determinate growth) bean or a short pole bean and a tall bush bean, by a three-factor hypothesis. The following values to be added to an initial value of three internodes were assigned to the factors: Factor *A* either homozygous or heterozygous added 10 internodes approximately, while factors *B* and *C* each added two internodes when homozygous and one when heterozygous. Results were explained factorially as follows:

Parent 1	*AABBCC* = 17 internodes or	*AAbbcc*	= 13 internodes
Parent 2	*aabbcc* = 3 internodes or	*aaBBCC*	= 7 internodes
F_1	*AaBbCc* = 15 internodes or	*AaBbCc*	= 15 internodes

Many new forms would naturally be produced in F_2.

Tschermak (1916) has brought together and summarized the

FIG. 60.—Flower structure of bean.

1. Small branch showing—*a*, developing pod; *b*, *c*, flowers in different stages of development.
2. Front view of fully opened flower—*a*, calyx; *b*, wing; *c*, standard; *d*, keel.
3. Enlarged keel.
4. Keel with outer part broken away to show—*b*, style; *c*, anther; *d*, undeveloped pod; *e*, ovary.
5, 6. Longitudinal and cross section of pod.
7. Enlarged stigma showing—*a*, stigma hairs.
8. Anther.

Size: 1, *n*; 2, about 2*n*; 3 to 8, greatly enlarged.

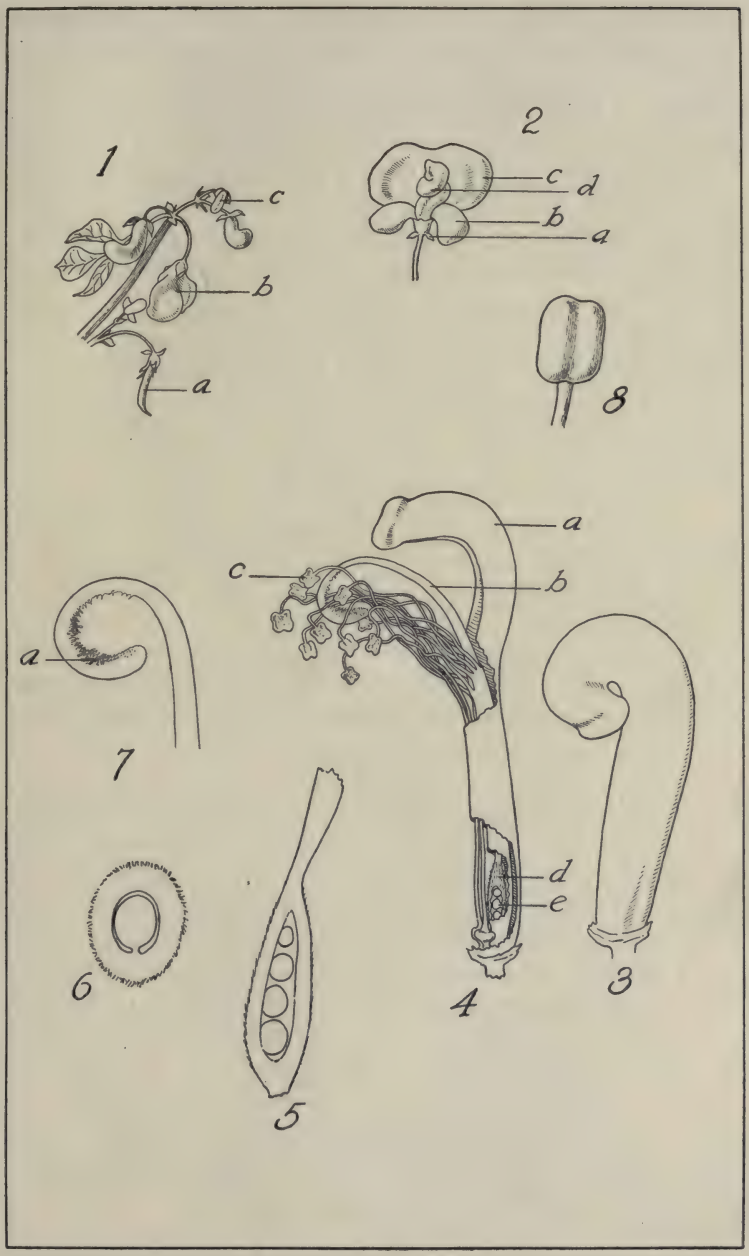


FIG. 60.

data on the inheritance of economic characters in the garden bean. Table LXII is made up from his summary.

TABLE LXII.—INHERITANCE IN THE BEAN

Contrasted characters	F_1 condition	F_2 behavior
Colored × white (flowers)	Colored	3:1
Green × yellow (unripe pods)	Green	3:1
Non-constricted × constricted (pods)	Non-constricted	3:1
Round × flat (pods)	Round	3:1
"Non-stringiness" × "stringy" (pods).	Intermediate or approaching non-stringiness	Stringy pods recessive (1 out of 4).
Blunt × sharp (pod ends)	Approaches blunt	Approaches 3:1.
Broad × narrow (pods)	Approaches broad	Segregation irregular.
Long × short (pods)	Approaches long	Segregation irregular.
Cylindrical × spherical (seeds)	Approaches cylindrical	Segregation irregular with spherical seeds constant.
Cylindrical × kidney-shaped (seeds)	Approaches cylindrical	Segregation irregular with kidney-shaped seeds constant.
Yellow × green (cotyledons)	Yellow (apparent on crossed seed)	3:1 (segregation apparent on F_1 plants).

The inheritance of resistance to various diseases is extremely important. One of the most injurious diseases of the bean is anthracnose (*Colletotrichum lindemuthianum*). Barrus (1918), as the result of an extensive study, was able to place beans in four groups with respect to susceptibility or resistance to this disease. Over two hundred varieties of beans commonly grown, besides many others, were tested. A considerable number of plants belonging to closely related genera were also examined. The cultures of anthracnose used for inoculating the varieties were obtained from widely separated geographical areas. By studying the reaction of the various cultures to each bean variety, two strains of anthracnose, alpha and beta, were discovered. With respect to their reaction to these two anthracnose strains, varieties of beans were placed in four groups:

(*ab*) Varieties susceptible to both strain alpha and strain beta.
(*aB*) Varieties susceptible to strain alpha but resistant to strain beta.
(*Ab*) Varieties susceptible to strain beta but resistant to strain alpha.
(*AB*) Varieties showing some resistance to both strains.

The most resistant variety of the last group is Wells Red Kidney. Results of crosses between varieties whose anthracnose

reactions are known indicate (McRostie, 1919; Burkholder, 1918) that resistance to either the alpha or beta strain is inherited as a simple dominant, involving but a single factor difference. It seems, therefore, very easy to produce resistant varieties to both strains by crossing and selection and thus to combine desirable economic characters and anthracnose resistance.

McRostie (1921) has recently published an interesting paper on further studies of disease resistance in common beans. The more extensive results obtained bear out the earlier views on the mode of inheritance of resistance to bean anthraxnose. The studies carried out show that bean mosaic susceptibility is inherited. In F_1 there was a partial dominance of susceptibility over resistance and in F_2 a segregation which indicated a two factor hypothesis. In crosses between susceptible and resistant varieties in relation to the dry root rot, caused by the fungus, *Fusarium martii phaseoli* Burk., there was a dominance in F_1 of susceptibility and a segregation in F_2 that appeared to be on a 9 : 7 basis. In nearly all cases resistant F_2 plants bred true to this character in F_3. Results of this nature show the great practical importance of the application of Mendelian principles to breeding for disease resistance. It seems very likely that a large part of our serious plant diseases will be controlled eventually by the production of disease resistant varieties.

TOMATO

Classification Characters and Inheritance.—The tomato belongs to the genus *Lycopersicum* of which there are several cultivated species. Tomatoes are classified on the basis of vine habit, either standard or dwarf, leaf type, period of maturity, size and color of fruits, and other characters. As a result of breeding experiments, many different combinations of characters have been made. Price and Drinkard (1908) were among the first investigators to report on the simple Mendelian behavior of certain tomato characters. Table LXIII, taken from similar ones compiled by Tschermak (1916) and Jones (1917), presents a brief summary of inheritance in the tomato.

Fruit shape is dependent on several factors according to Crane (1915) and Groth (1912, 1915). Some of the foliage characters are also somewhat complicated in their inheritance (Groth, 1911). The inheritance of each of the other characters listed in the table is dependent on single factor differences.

TABLE LXIII.—INHERITANCE OF CHARACTERS IN THE TOMATO

Characters	Dominant	Recessive
Fruit shape	Spherical	Pear-shaped
Fruit shape	Roundish conical	Roundish compressed
Loculation of ovary	Two-loculed	Many-loculed
Endocarp color	Red	Yellow
Epicarp color	Yellow	Colorless
Fruit surface	Smooth	Pubescent
Leaf margin	Serrate (normal or fine leaf)	Entire (potato or coarse leaf)
Leaf type	*Pimpinellifolium* type	*Esculentum* type
Leaf color	Green	Yellow
Inflorescence type	Simple	Compound
Vine habit and leaf surface	Standard, smooth	Dwarf, rugose
Height of plant	Tall or normal	

The F_2 segregation ratio is 3:1. Jones (1917) has pointed out that the data of Hedrick and Booth (1907) and Price and Drinkard (1908) show linkage relations between the factors for vine habit and fruit shape and also between those for leaf color and loculation of ovary.

Heterosis in the F_1 generation of certain tomato crosses and its commercial possibilities for increased production have been pointed out (Wellington, 1912; Hayes and Jones, 1916). Groth, of the New Jersey State College Experiment Station, made a study of size inheritance in the tomato fruit. The results are explained by what the author (1914) terms "Golden mean." If (a) and (b) represent the respective magnitudes or volumes of size characters of the parents, the F_1 is represented by $\sqrt{ab}$ rather than $(a+b)/2$. This hypothesis was put forward as non-Mendelian and in explanation of results in size inheritance frequently attributed to multiple factors. Emerson (1914*b*) has shown that the hypothesis is essentially based on multiple factors.

PEPPERS

Classification Characters and Inheritance.—Garden peppers which are commonly grown for pickles or for condiments belong to the species *Capsicum annuum*. From the standpoint of their utilization as food, peppers may be divided roughly into two groups—hot and mild, depending on flavor. Mild peppers are

frequently used green for slicing or stuffing, whereas hot peppers more often serve as a condiment in spice mixtures. Number of days to mature is usually given by seeds-men in describing varieties. Color, size, shape, and uniformity of fruit are other important commercial characters.

A limited number of inheritance studies with this vegetable have been made. Webber (1911) and Ikeno (1913) report the behavior of certain characters in the second generation after a cross. Below is given a tabular summary of a part of the results obtained.

TABLE LXIV.—INHERITANCE IN THE PEPPER

Contrasted characters	F_1 condition	F_2 behavior
Violet × white (flower)...	Violet (considerable variation in amount of violet coloring)	3:1
Violet flower associated with violet coloring in leaf-stem and ripe fruit. White flower associated with green leaf and stem except for a dark spot near attachment of petiole.		
Umbel × non-umbel (inflorescence)	Non-umbel	3:1
Red × orange (ripe fruit)..	Red	3:1
Pubescence × non-pubescence (stems and leaves)	Less hairy than hairy parent	15 pubescent:1 non-pubescent
Pungent × sweet (fruit)...	Pungent	Approx. 3:1

In the inheritance of size of leaf, Webber obtained results which clearly indicated that several factor differences were involved and a like result was obtained by both Webber and Ikeno with regard to size of fruit. The character of the peduncle, whether erect or recurved, was found by Ikeno to be dependent on a single factor difference, erect being the recessive condition when the fruit had ripened. During the flowering stage and early development of the fruit the heterozygous individuals for this character-pair showed dominance for the erect peduncle.

Methods of Breeding Self-Fertilized Vegetables.—The vegetables discussed above together with others which are naturally self-fertilized or which will produce ample viable seed when selfed may be considered as a single group from a breeding standpoint. The method of breeding this group is identical with that already outlined for naturally self-fertilized crops and hence

need not be repeated here. Yield, quality, and disease resistance are the three most important economic characters. To bring about a desirable combination of these characters, both selection and hybridization have been practiced.

Selection has been used by Edgerton (1918), of the Louisiana Agricultural Experiment Station, to isolate tomatoes resistant to wilt (*Fusarium lycopersici*). The improved technic followed is worthy of consideration. Seeds of a particular variety were planted in soil which had been sterilized previously and then inoculated with a pure culture of the wilt-producing organisms. When seedlings showed wilt infection they were pulled and discarded. Only plants which showed resistance were transplanted to the field. Tomatoes had grown continuously for eight or ten years on this field and it was known to be heavily infected with the wilt fungus. The use of this method permits a smaller acreage and insures the contact of each plant with the wilt organism. A selection made from a row of Acme grown in 1909 named "Louisiana Wilt-Resistant" was extremely wilt resistant but possessed other characters which made it undesirable for Louisiana conditions. Selections from the progeny of crosses between this form and Earliana showed considerable promise.

Durst (1918) reported the result of five years' selection for resistance to *Fusarium* of tomatoes. Varieties were found to differ a great deal in their resistance and unfortunately the most resistant ones produced poor fruit. After five years, some of the better strains stood up in soil which proved fatal to the original varieties. In addition to disease resistance, the selections also showed good yielding ability. Of seventy-four lots grown one year the highest fourteen yields were produced by selected strains.

Whether selection alone or hybridization and selection together are to be used as a means of improving a crop is dependent upon the nature of the material. If the character combination is not already present, the only practical means of bringing it about is crossing followed by selection.

Cross-Fertilized Vegetables

Crops have previously been classified as belonging to four groups according to their mode of reproduction. Cross-fertilized vegetables may be roughly divided into three main divisions;

1. Those which are normally cross-pollinated but which set seed freely on selfing and show no evidence of sterility.
2. Those which are wholly or partially self-sterile.
3. Those which are cross-fertilized owing to the dioecious condition.

Much more study of the mode of pollination of vegetables is necessary before it is possible accurately to classify vegetables according to their mode of reproduction. The crops here considered have been purposely chosen as illustrations of breeding results within these three groups.

RADISH

Origin, Inheritance, and Breeding.—The cultivated radish, *Raphanus sativus*, was grown by the ancient Greeks and Romans. There has been considerable discussion as to its origin. Some writers have thought that the cultivated form with its fleshy root arose directly from *R. raphanistrum*. This belief was apparently substantiated by experiments in which the wild form was grown under cultivation and after several years cultivated radishes were obtained. Riolle (1914) tested this hypothesis by a controlled experiment. The wild form was grown under cultivation and self-fertilized. Three years of selection failed to produce roots which resembled the fleshy roots of *R. sativus*. On the other hand, when the wild and cultivated forms were both grown on the same plot and seed was saved from the wild form, it was found to be an easy matter, after three years' selection, to obtain roots which resembled the fleshy roots of *R. sativus*. These results were believed to be due to natural crossing of the wild and cultivated forms. This hypothesis was tested by making an artificial cross. Segregation for root condition occurred in F_2. This led Riolle to conclude that former experiments in which cultivated radishes were obtained from the wild through selection were best explained through natural crossing.

R. sativus roots contain sugar while wild roots contain no sugar. F_1 crosses contain less sugar than the cultivated forms. The presence of starch in the root of the wild radish, particularly in the bark, is a character which separates it from the cultivated varieties. This proved a dominant in crosses. Cultivated radishes show various color intensities. Color is apparently inherited in much the same manner as in other crops. Individual

radish plants were grown under cover by Riolle and self-fertilized seed was produced in abundance. This led Riolle to suggest that homozygous strains be first produced. These would then furnish material for accurate inheritance studies as well as be of much value for economic breeding purposes. On the other hand, Stout (1920) has stated that there is considerable self-sterility in the cultivated radish. Up to the present, mass selection has been most frequently used as a means of breeding radishes (Tschermak, 1916).

BEETS

Inheritance and Breeding.—Both garden beets and sugar beets belong to the species *Beta vulgaris.* Kajanus (1913) made a study of the inheritance of root forms in mangels and sugar beets. In general, the F_1 roots were intermediate between the parental forms. Sugar beet crosses in which wedge-shaped forms were involved proved to be exceptions. Wedge-shape was completely dominant over walnut-form and also over long, somewhat slender roots (post-shape). The other beet shapes studied were oval and round. Most of the ratios obtained in F_2 could be satisfactorily explained on the basis of four factors—two involving length of root and two concerned with form.

A marked increase in the sugar content of the sugar beet was produced by Vilmorin through the application of the progeny test method (see page 119). There is some difference of opinion regarding the ease of producing self-fertilized seed. Shaw (1915) demonstrated that the sugar beet, isolated (two miles from any other beet plants), will set some seed. To what extent self-sterility is a factor is unknown. The production of homozygous forms through self-fertilization would seem worth trying as a means of obtaining homozygous material for breeding studies. This method seems a logical procedure for all vegetables which are naturally cross-fertilized but which also set seed freely under conditions of self-fertilization.

Mass selection is often used in breeding beets. Only those roots which come up to an adopted standard are stored over winter and set out the following spring to become the seed-producing plants. Carrots and parsnips, when bred by mass selection, are handled in a similar manner. Although varieties of any one of the crops, beets, carrots, or parsnips, freely intercross, there is no crossing between the three different kinds of

vegetables (Malte and Macoun, 1915). This fact may be utilized in making planting plans.

CULTIVATED VEGETABLES OF THE GENUS BRASSICA

Cabbage and several other vegetables such as cauliflower, brussels sprouts, kohl-rabi, and rutabagas, belong to the genus *Brassica*. Few inheritance studies have been made with this group of vegetables. Cabbage has received more attention from a breeding standpoint than the others.

Inheritance.—The evidence so far accumulated indicates that cabbage belongs to the cross-fertilization obligatory group. Price (1911–1912) and Jones and Gilman (1915) were not able to produce self-fertilized seed under a bag. Tschermak (1916) maintains that many of the kinds of vegetables belonging to the cabbage group freely intercross when in close proximity at blooming time. The above facts are fundamental and show the method of breeding which must be used. They may also aid in explaining some unusual inheritance results.

Price crossed varieties of crinkled-leaf and smooth-leaf cabbage, obtaining dominance for crinkled leaf in F_1 with no segregation of this character in F_2 ,*i.e.*, all plants (419) had crinkled leaves. With respect to size, shape, and solidity of heads, color of foliage, and length and thickness of stem, considerable more variability was obtained in F_2 than in F_1. In a cross between a crinkled-leaf cabbage and a cauliflower, the thick, leathery leaf of the latter was dominant in F_1 and was the only apparent leaf characteristic in F_2. Head cabbage crossed with headless produced nothing but headed forms both in the F_1 and F_2 generations. As to type of head, the cabbage or leafy form was found to be dominant over the type of head of the cauliflower. In F_2 the cabbage head form was maintained without apparent segregation. Crosses between cabbage and brussels sprouts gave F_1 and F_2 generations identical with respect to habit of growth, *i.e.*, all were determinate. Axillary buds were more common in the hybrids than in ordinary cabbage. The thick stem of kohl-rabi was found to be dominant in a kohl-rabi-cabbage cross and a limited number of F_2 individuals showed no segregation of this character.

Sutton (1908) crossed reciprocally kohl-rabi and Drumhead cabbage, obtaining, in F_2, 3 non-kohl-rabi plants to 1 resembling

kohl-rabi. The parental forms did not appear in the F_2 generation. Drumhead cabbage crossed with Thousand-headed kale produced 204 plants in F_2. Of these, 176 resembled a dwarf type of Thousand-headed kale with leaves broader than usual and fewer branches; 26 resembled cabbage; and two plants were much like brussels sprouts.

The difficulty of a study of inheritance in the *Brassica* genus arises from the heterozygous condition of many forms and the self-sterile condition. Before the results are accepted as examples of non Mendelian behavior, a criticial study in which all facts are considered should be made. In cabbage there is apparently a complicated inheritance. The above results are satisfactorily explained on a multiple-factor hypothesis. In crossing heterozygous forms, the F_1 generation may be as variable as the F_2. In the inheritance of any particular character, the number of factor differences may be so large as to make the appearance of parental forms improbable in a small F_2 generation.

Breeding.—The breeding of cabbage resistant to yellows (*Fusarium conglutinans* Wollenw.) at the Wisconsin Experiment Station (Jones and Gilman, 1915) is of great economic importance. Less than a decade ago, truck farmers in certain sections of Wisconsin were so discouraged from the ravages of yellows that they were about to abandon cabbage growing. The method of producing resistant cabbage strains may be briefly summarized. It had been noticed that there were usually a few plants which escaped the disease in a field where nearly all plants were badly infected with the organism. These apparently resistant plants were selected on the basis of type. After storing over winter, all that were of the same general type were planted together and were far enough removed from any other similar planting to insure against contamination by foreign pollen. Selfed seed was not obtained but most plants not bagged set seed abundantly. Some plants were eliminated because of low seed production. Progeny of the retained plants were grown separately and their resistance to yellows was tested. In this way several strains of cabbage highly resistant to yellows have been produced. Further studies have been reported and numerous resistant varieties have been produced (Jones et al, 1920). The writers emphasize the fact that resistance is not absolute and that enviromental factors influence very markedly the development of the disease. They state, however, that:

"By following the proper methods any skillful cabbage grower who has Fusarium sick soil may either undertake with reasonable confidence to develop a resistant strain of his own, or having secured one of these resistant strains he can maintain its resistance and produce his own seed."

ASPARAGUS

Asparagus (*Asparagus officinalis*) is dicœcious in habit of flowering altho hermaphrodite plants have been discovered (Norton, 1911-1912). With this vegetable, cross-pollination is usually necessary for seed production.

Rust-Resistant Asparagus.—The fungus, *Puccinia asparagi*, has occasioned a great deal of alarm among commercial asparagus growers, particularly those of the eastern United States. This rust differs from that occurring on the small grains in that all stages of the rust occur on the asparagus plant. At the invitation of Massachusetts growers, the United States Department of Agriculture in coöperation with the Massachusetts Agricultural Experiment Station undertook to produce a resistant variety. Norton (1911–1912, 1913) has reported on this investigation. Because of the dicœcious habit of asparagus it was necessary to select two kinds of plants—male and female. Selections were based on rust resistance, *i.e.*, only plants which showed a high degree of resistance were chosen. In 1909 the first test of the transmission of relative rust resistance was made. Twelve lots saved from as many plants showing various degrees of rust resistance were planted in duplicate in short rows. After the young shoots appeared they were dusted several times with fresh uredospores. Later in the season observations were made on the degree of infection. The results are given in Table LXV (Norton, 1913).

Table LXV shows clearly that rust resistance is inherited. Various artificial crosses were made between forms showing rust resistance. The progeny of some of these crosses proved highly resistant and in some cases were more resistant than the parents. By this method several strains of asparagus with a high degree of resistance have been produced. In the production of a new form a male plant obtained in 1910 from a lot of New American of unknown origin proved of marked ability in transmitting vigor and rust resistance to the progeny. The female plants known as Mary and Martha were selected from the variety Reading

TABLE LXV.—TRANSMISSION OF RUST RESISTANCE IN ASPARAGUS

Row	Source of seed	Type of plant	Rank of seedlings in resistance		
			First lot	Second lot	Average
1	*A*1–6	Badly rusted, near rusty bed	7	9	8.0
2	*A*3–61	Very resistant female	6	5	5.5
3	*A*4–7	Resistance good	3	7	5.0
4	*A*4–17	Resistance fair	10	8	9.0
5	*A*7–5	Resistance good	4	3	3.5
6	*A*7–15	Resistance good	2	4	3.0
7	*A*7–25	Resistance good	5	2	3.5
8	*B*24–27	Very rusty	11	10	10.5
9	*B*24–28	Very rusty	9	11	10.0
10	Old field	Rusty	12	12	12.0
11	Old field	Resistant	8	6	7.0
12	Frank Wheeler old bed	Best resistant female	1	1	1.0

Giant. Two or three other females have been selected and the crossed seed obtained from these selected plants has been distributed under the name Washington asparagus (Norton, 1919). Some of these strains are now being offered for sale by commercial seedsmen.

Norton suggests the following method for breeding asparagus; After two mated plants have proved their value by the progeny test, they should be dug up and propagated by crown division. These clones are isolated together and retained exclusively as breeding stock. Isolation may be accomplished by a fine-meshed cage to prevent the entrance of bees or by planting at a safe distance from other beds of asparagus. Producing seed in a greenhouse by hand pollination has also been found successful.

ECONOMIC CUCURBITACEÆ

Introduction and Classification.—The family *Cucurbitaceæ* is of considerable historical interest. Sageret (1826) and Naudin (1856, 1859*a*, 1859*b*), two pre-Mendelian workers, made extensive hybridization studies with some species belonging to this family. Naudin made a species classification on the basis of genetic behavior which is accepted at the present time. All the forms which cross readily were placed in the same species group.

Cucumis sativus—Cucumber

Cucumis melo — Muskmelon, cantaloupe

Cucurbita pepo —Pumpkin, gourd, summer squash, and varieties of winter squash. Peduncle hard and ridged.

Cucurbita maxima—Large field squash and winter squash. Peduncle soft and fleshy.

Cucurbita moschata—Squash. Little grown in United States. Peduncle much enlarged where attached to fruit.

Citrullus vulgaris—Watermelon, citron.

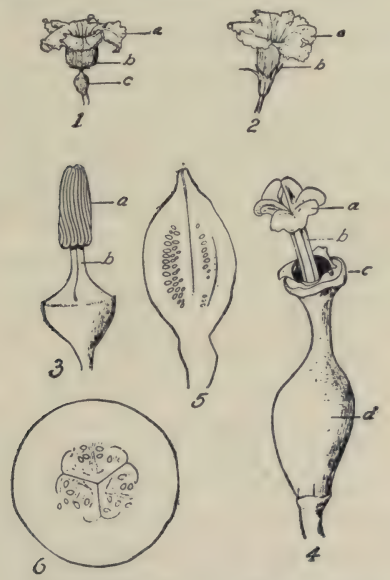


FIG. 61.—Structure of flowers of squash.

1. Female flower—*a*, corolla; *b*, calyx; *c*, fruit.
2. Male flower.
3. Male flower with calyx and corolla removed.
4. Female flower with calyx and corolla removed showing—*a*, stigma; *b*, style; *c*, point of attachment of calyx and corolla; *d*, undeveloped fruit.
5, 6. Longitudinal and cross sections of fruit.

Size: 1, 2, $\frac{1}{4}n$; 3, 4, $\frac{1}{2}n$.

Cummings (1904) experienced no great difficulty in crossing Golden Custard (♀) with Crookneck (♂), varieties of squashes belonging to *C. pepo*. The reciprocal cross proved difficult, only five out of 284 pollinations producing fruit with viable seed. A histological examination revealed the fact that the male generative

nucleus of Custard penetrated the ovary of Crookneck and took up a position which, in many cases, was in close proximity to the egg cell but for some reason fusion did not occur in most cases.

Bailey (1890), as the result of many artificial pollinations, concludes "that the field pumpkins and the summer and fall types of bush squashes (*C. pepo*) do not cross with the running squashes of the Hubbard, Marblehead, Boston Marrow, turban, and mammoth types (*C. maxima*)." In the Cyclopedia of American Horticulture, Bailey (1900) states that *C. moschata* and *C. pepo* may be crossed artificially but it is doubtful if they cross naturally. *Cucurbitaceæ* in general are monœcious and largely dependent on insects for pollination.

Immediate Effect of Pollination.—There is a popular belief widely disseminated that pumpkins and watermelons should not be grown in close proximity to one another because of the immediate effect of cross-pollination. A similar belief exists with regard to cucumbers and muskmelons. Evidence accumulated by various plant breeders shows that this idea is not founded on fact. The work of Bailey at Cornell and Pammel at Iowa may be cited. The former (1890) was unable to find any immediate effect of cross-pollination between varieties of *C. pepo* and likewise between varieties of *C. maxima.* Bailey not only was unable to demonstrate any immediate effect of pollen in varieties which could be crossed but he was even unable to produce crosses between cucumbers and muskmelons. Ninety-seven flowers of several varieties of melons were pollinated with different varieties of cucumbers. Not a single fruit set. Twenty-five reciprocal pollinations were also made. One fruit developed but produced no seed. The setting of parthenocarpic fruit without fertilization is not an infrequent occurrence in cucumbers. Pammel (1892), in an intermingled planting of varieties of each of the following species, *Citrullus vulgaris, Cucumis melo, Cucurbita maxima, Cucumis sativus,* and *Cucurbita pepo* provided excellent facilities for inter-specific pollinations. Neither the watermelons nor the muskmelons showed contamination. Some hand pollinations between species were made, but no cross-fertilization was obtained.

The variability in flavor of commercial varieties of melons is undoubtedly partly responsible for the erroneous belief that they may be contaminated by other species of cucurbits growing in close proximity. At the Connecticut Station an extensive varietal test was made. Most of the varieties were of very inferior quality even though they were exposed only to

muskmelon pollen. Even if crossing occurred, there is no conclusive evidence that xenia would result.

CUCUMBER

Wellington, (1913) studied the inheritance of the following characters: color, size, number of spines, smooth or rough skin, and obtained ratios indicating monohybrid segregation. Smooth skin and small spines, few in number, appear to be linked. Heterosis shown by increased number or size of fruit, has been observed in the F_1 of certain cucumber crosses (Hayes and Jones, 1916). The F_1 of a cross (Reeves, 1918) between American type (20 per cent parthenocarpic) and English type (normally parthenocarpic) showed 20 per cent parthenocarpy.

MUSKMELON

Lumsden (1914), of the New Hampshire Agricultural Experiment Station, has made rather extensive studies of inheritance in the muskmelon. The following tabular statement gives a summary of his work:

TABLE LXVI.—INHERITANCE IN THE MUSKMELON IN A CROSS BETWEEN THE VARIETIES SUTTON'S SUPERLATIVE AND DELICES DE LA TABLE

Characters	No. of F_1 plants	F_1	No. of F_2 plants	F_2 ratio
Color of skin	..		..	Yellow : green
Yellow × green	1	Yellow	79	2.76 : 1
Form of fruit	..		..	Round : elliptical
Round × elliptical	1	Round	79	2.76 : 1
Ribbing	..		..	5–45 per cent. ribbing : 46–100 per cent. ribbing
Ribbed × non-ribbed	1	Ribbed	79	1 : 1.82
Netting	..		..	5–45 per cent. Netting : 46–100 per cent. netting
Netted × smooth	1	Netted	79	1 : 1.63
Size of seed	..		..	Large : small
Large × small	1	Large	79	2.95 : 1
Size of fruit	..		..	Large : small
Large × small	1	Large	79	2.59 : 1

These data show that all the characters studied segregated in the second generation. There is some indication that the contrasted characters in color of skin, size of seed, size of fruit, and form of fruit are each separated by a single main factor difference. In a cross between varieties producing round and elliptical fruits respectively the F_1 fruit was recorded as round, while the F_2 gave a ratio of 2.76 round to 1 elliptical. The other two characters, netting and ribbing, indicate more complex inheritance. Delices de la table (♂) has deep ribbing and no netting; Sutton's Superlative (♀) has no ribbing and pronounced netting. The F_2 generation showed a variation of from 5 to 100 per cent. with respect to each character.

SQUASHES AND GOURDS

Emerson (1910), while at the Nebraska Experiment Station, made a study of size inheritance in a cross between Yellow Crookneck and White Scallop summer squashes. He found that length of neck and diameter of bowl were intermediate between the parents in F_1. The second generation showed a complete series of dimensions and shapes from one parent to the other. The same investigator crossed Striped Spoon gourd with Filipino Horned gourd. Results similar to those of the squash cross were obtained.

WATERMELON

One of the most serious handicaps to the production of watermelons in the Southern States is the presence of wilt, due to an organism, *Fusarium niveum*. "Citron" or "stock melon," so-called locally, is a non-edible variety of *Citrullus vulgaris* resistant to wilt. Orton (1911) conceived the idea of crossing this form with edible forms. He hybridized Eden, a good quality melon, with citron. The F_1 was very vigorous and of intermediate type. Between three and four thousand F_2 plants were grown and ten fruits selected on the basis of resistance and quality. After selecting the resultant progeny for several years the variety Conqueror was isolated. It is disease resistant, has a tough rind, and does not sunburn easily. The flesh is juicy and of good quality, although not equal to the finest. These studies were made in South Carolina. It was found that Conqueror

retained its resistance when grown in Iowa but seemed to lose it when grown in Oregon, on the Pacific Coast. No very satisfactory explanation has been offered for this phenomenon. It is possible that a similar condition exists with flax wilt.



FIG. 62.—A strain of Hubbard squash isolated by self-fertilization which is comparatively uniform for the production of large fruits of uniform shape. Minnesota Exp. Sta. (*Courtesy of Bushnell.*)

Flax strains resistant to wilt seem to lose their resistance when grown for a few years in wilt-free soil.

Breeding Cucurbitaceæ.—Each botanical species of this family in most cases constitutes a freely inter-crossing group of

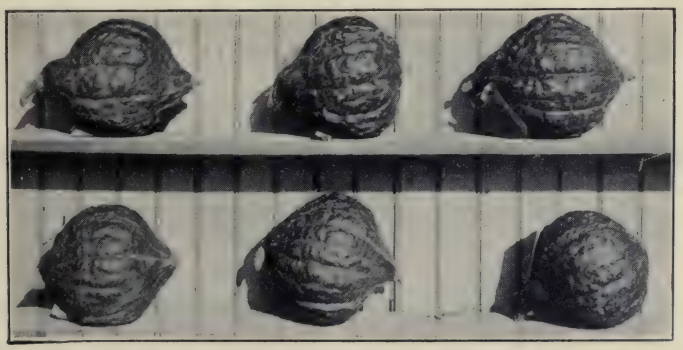


FIG. 63.—A small fruited strain isolated from a commercial variety of Hubbard squash by self-fertilization. Minnesota Exp. Sta. (*Courtesy of Bushnell.*)

varieties. The monœcious character of the plant encourages cross-fertilization. In spite of these facts the authors believe that in some cases progress may be made by breeding methods

recommended for self-fertilized crops or more specifically for crops which yield ample seed on selfing. When such a plan is adopted for naturally cross-fertilized crops it becomes necessary to insure selfing by artificial means. By reducing ordinary varieties to pure lines, a much more exhaustive study of the material at hand may be made, and on the basis of this study desirable combinations affected by hybridization or pure lines of commerical value may be isolated. The method which is adopted after the isolation of homozygous lines through self-fertilization will depend on the degree in which vigor is lost as a result of selfing. That homozygous lines may be isolated in squashes is a demonstrated fact, the result of three years' study as carried on by John Bushnell, of the Minnesota Station. Some lines which are comparatively uniform appear vigorous while others are less vigorous. Types for markedly different characters which are relatively uniform have been isolated.

CHAPTER XVIII

FRUIT BREEDING

The improvement of fruit crops offers an interesting field of study for the trained investigator. Many fruits are in a complex heterozygous condition. For this reason and because fruits are propagated by asexual methods Mendel's law does not have here the same value as for the breeder of self-fertilized crops. There are also many fruit crops which are totally self-sterile so that cross-pollination, either natural or artificial, is essential to the production of fruit. Unlike an annual crop the individual fruit tree often takes many years to grow before fruiting. For these reasons methods of handling are often of much greater importance than methods of breeding. It is, therefore, of utmost importance that the student first make an intensive study of the botanical relatives, methods of culture, varieties, and environmental necessities of the crop before undertaking breeding operations.

ORIGIN AND ANTIQUITY OF SOME FRUITS[1]

Wild fruits without doubt played an important rôle in the food supply of primitive man. As the art of agriculture came to be developed because of the necessity of obtaining enough food to supply the increasing human population, the fruit crops were gradually introduced into cultivation. Some of our most prized fruits, as the apple, grape, and plum, have been cultivated since earliest times; while others, as the strawberry, black raspberry, and blackberry, have been brought under cultivation since America was discovered.

The wild species from which our fruits have been developed may still be found today. Wild plums may be found in nearly every state of the United States, while in central and northern Asia the wild relatives of apples, pears, apricots, cherries, and plums are of frequent occurrence.

The wild crabs are found in abundance, in both the Eastern and the Western Hemispheres. As the cultivated European

[1] A paper by White (1916) has been used very freely in this discussion.

varieties gave good results when introduced into the United States, the breeding of apples has not been seriously undertaken until comparatively recent times. The cultivated varieties are very numerous. Our pears were developed from two very different wild species, *Pyrus communis*, the wild pear of western Asia and Europe and the hard, gritty sand pear of northern China. *P. communis* is the source of our eating pears, such as the Bartlett, while inter-species crosses furnished our cooking and winter pears.

Peaches were first developed in China. When one compares the little hard, bitter wild peach of China and our cultivated varieties the results of early breeding are strikingly illustrated.

There are three groups which are commonly accepted as the ancestral forms of our cultivated plums: (1) The thorny wild European species which produces dark purple fruits about the size of a pea. These are the source of our prune varieties. (2) North American native wild plums which have a very juicy flesh without much meat. Several species are recognized (Wight, 1915). (3) A Chinese-Japanese wild species. Many of the cultivated varieties of plums are largely of hybrid origin.

There are over 120 wild species of cherries which are native to Asia and from 200 to 1,500 wild species of raspberries and blackberries. The variation in type of the wild red raspberries of New England is a good illustration of a wide diversity of forms. Some of these are probably results of crosses with escaped cultivated varieties. Natural hybridization certainly played a large part in the evolution of such fruits and the selection of promising wild seedlings furnished the major part of our cultivated varieties.

Fletcher (1916) has described 1879 varieties of strawberries which originated in North America and 26 European varieties which have attained prominence in this country. The strawberry is largely a hybrid product of four or more species.

The citrus fruits are all of Asiatic origin. Present cultivated varieties have for the most part been produced during the last 100 years. The grapefruit industry of the United States has been developed in the last 25 years. This fruit, which is a native of islands lying to the south of Asia, was introduced into the West Indies early in the eighteenth century and more recently from the West Indies into Florida. Table LXVII, which is part of a table published by White (1916), is a summary statement of the source

and the length of time under cultivation of some of our most highly prized fruit crops.

TABLE LXVII.—ORIGIN, PROBABLE LENGTH OF TIME OF CULTIVATION, AND COMMENTS ON SOME CULTIVATED FRUITS (AFTER WHITE, 1916)

Name	Date	Origin	Remarks
Apple	*A*	E. Europe, W. Asia	Very different type common to China.
Apricot	*A*	Central Asia, China	Wild species variable.
Blackberry	*F*	United States	Wild species very variable.
Blueberry	*F*	E. and N. North America.	Four species, often confused with huckleberry.
Cranberry	*F*	E. and N. North America	Cultivated for about 100 years.
Currant, red	*C*	Northern Hemisphere	White and yellow varieties are forms.
Cherry, sour	*B*	Asia Minor, S.E. Europe (?)	
Cherry, sweet	*B*	S. Europe, E. Asia	
Grape, Old World	*A*	West temperate Asia	California and Old World grape.
Grape, New World	*F*	North America	Many probably hybrids.
Gooseberry	*C*	N. Europe, N. Africa, W. Asia, United States	Old and New World species distinct.
Grapefruit	*B*	Malayan and Pacific Islands east of Java	Largely cultivated in United States.
Lemon	*B*	India	
Orange, sweet	*C*	India	Numerous hybrids with other species.
Peach	*A*	China	Hundreds of varieties.
Pear	*A*	Temperate Europe and Asia, N. China	Two species and hybrids between them.
Plum	*A*	S. Europe, W. Asia, N. America.	Much hybridized group.
Raspberry, red	*C*	N. Europe, Asia, N. America	Varieties and hybrids of two species.
Raspberry, black	*F*	Middle North America	
Strawberry	*F*	Temperate N. America, Pacific Coast of N. and S. America, Europe	At least three species involved.

A, cultivated for more than 4,000 years.
B, cultivated for more than 2,000 years.
C, cultivated for less than 2,000 years in the Old World.
F, cultivated since the discovery of America. Often only very recently.

The mode of origin of some of the better United States fruit varieties has been compiled by Dorsey (1916) from the New York Agricultural Experiment Station fruit monographs. A summary statement is presented in Table LXVIII.

These data show that nearly 85 per cent. of the commercial fruit varieties of apple, cherry, plum, and grape have been obtained by selecting promising chance seedlings, that one parent was known for a little more than 10 per cent. of the varieties described,

TABLE LXVIII.—ORIGIN OF VARIETIES OF APPLE, CHERRY, PLUM, PEACH AND GRAPE

Fruit	Both parents known	One parent known	Neither parent known	Origin as bud sports	Total
Apple	3	39	588	4	634
Cherry	20	61	1,064	0	1,145
Grape	74	57	72	0	203
Plum	49	108	524	1	682
Peach	2	13	69	1	85
Total	148	278	2,317	6	2,749

while over 5 per cent. of the commercial varieties originated from crosses in which both parents were known. Only six out of 2,749 varieties are known to have originated as bud sports.

SOME EARLY STUDIES IN FRUIT IMPROVEMENT[1]

The preceding discussion gives some idea of the great number of varieties of our fruit crops. While many of these are from chance seedlings, a considerable percentage resulted from definite attempts to produce improved forms.

Von Mons.—One of the earliest horticulturists was a Belgian by the name of Von Mons, who was born in 1765 and died in 1842. He was a chemist but followed horticulture as an avocation. His studies were carried out for the purpose of proving the truth of certain philosophical theories. While he did not succeed in substantiating the theories, his work was of considerable value to horticultural science and practice. His most important studies were with pears. In 1823 there were 80,000 seedlings in his nursery. About this time he issued a catalog in which 1,050 pears were described by name or number. Of these, 405 varieties were of his own production. His practice was to sow, select, and resow, and without doubt a part of his great accomplishments was a direct result of cumulative selection.

Knight.—Thomas Andrew Knight has already been mentioned as a man who contributed much to the art of plant breeding. He was born in England in 1759 and died in 1838. A part of his work was carried on with such fruit crops as apples, pears, and peaches.

[1] For an account of the evolution of American fruits the reader is referred to BAILEY, 1898; MUNSON, 1906.

He emphasized the value of crossing as a means of producing improved forms for he believed this method was more rapid than Von Mons' selection practice.

American Pomology.—Throughout the nineteenth century American pomologists made great progress in the improvement of fruits. While many American named varieties occurred as chance seedlings, others were the result of careful breeding. The strawberry and grape are examples of fruits in which many of the varieties are a result of controlled breeding. Selection and crossing both played important parts in the improvement of varieties. Hovey was one of the best known of the early strawberry breeders who worked during the first half of the nineteenth century.

The production of improved American varieties of grapes well illustrates a common method of the production of new fruits. Old World grapes did not succeed in the greater part of the United States, as European varieties proved very susceptible to diseases, particularly mildew. The production of American varieties from native wild species gave us many of the cultivated types. Some of the best of the early varieties arose as chance seedlings. Concord was thus discovered by Ephraim W. Bull and introduced about 1853. It has been frequently used as a parent for the production of the improved forms. Some improved forms have resulted from crosses between native and European varieties, Delaware being generally thought to have been so produced.

With the plum, as with the grape, the native American species have furnished the source from which a large part of the American varieties have been produced (Wight, 1915). Several wild species have been used and frequently the varieties which have proved best adapted to a given locality have been produced from the wild form which is native to the same region.

SOME CONSIDERATIONS OF FRUIT BREEDING

Fundamental laws of heredity furnish the same foundation for a development of correct breeding technic in the fruits as with other crops. There are, however, some factors which modify breeding methods. For example, a single tree takes up considerable field space and thus has a greater value than a single plant of wheat or corn. In comparing varieties and clonal lines the question of soil heterogeneity must be considered for this is

probably a frequent cause for the variation in yield from different trees of the same variety when grown in the same orchard. Self-sterility, which is so prevalent among fruit crops, often prevents the production of homozygous material; while the use of heterozygous material does not allow the breeder to make systematic crosses with a knowledge of the genetic constitution of the parents. In spite of these difficulties which the fruit breeder must face, there has been a consistent attempt to use fundamental breeding principles and at present methods are becoming somewhat standardized. The advantage which comes to the breeder from the fact that an improved variety may be propagated asexually and need not be reduced to a homozygous condition, tends to offset other difficulties Some of the more general problems will be here illustrated.

Overcoming Soil Heterogeneity.—Batchelor and Reed (1918) have made an interesting study of variability in orchard plots. They used orange, lemon, walnut, and apple trees in the investigation. From 224 to 1,000 trees of each of the different fruits were studied and the coefficient of variability for yield of single trees determined. The coefficient of variability of the clonal varieties ranged from 29.72 to 41.23 per cent. Thirty-five per cent. might be considered a fair average. Multiplying this by 0.6745 gives 23.6, the probable error in percentage of the mean.

The effect on the coefficient of variability of increasing the number of trees in a plot was studied; a comparison of plots containing 1, 2, 4, 8, 16 and 24 trees being made. Table LXIX gives an average of tests with oranges, lemons, apples, and walnuts. The results are based on a study of more than 2,000 individual trees.

TABLE LXIX.—EFFECT OF INCREASING THE NUMBER OF TREES PER PLOT

Number of trees per plot	Average coefficient of variability	Average reduction of coefficient of variability by increasing number of adjacent trees per plot	
		Increase from	Average reduction
1	37.78±0.52		
2	30.89±0.55	1 to 2	6.89±0.76
4	26.76±0.62	2 to 4	4.13±0.83
8	24.27±0.77	4 to 8	2.49±0.99
16	22.58±1.01	8 to 16	1.69±1.27
24	19.74±1.08	16 to 24	2.84±1.48

From these results the conclusion is reached that eight trees is about the correct number which should be used in a plot.

The question of replication, *i.e.*, the systematic distribution of plots over the field, is taken up. Results computed for four- and eight-tree units are given for oranges, apples, walnuts, and lemons. Table LXX gives an average of data from these crops.

TABLE LXX.—EFFECT OF REPLICATION IN FOUR- AND EIGHT-PLOT UNITS

Four trees in a unit	Eight trees in a unit	Number of systematically replicated plots
26.76 ± 0.60	24.27 ± 0.77	1
15.12 ± 0.47	12.84 ± 0.56	2
13.58 ± 0.53	11.27 ± 0.63	3
9.29 ± 0.40	9.54 ± 0.57	4
8.40 ± 0.40	7.95 ± 0.49	5
8.49 ± 0.49		6

The conclusion seems warranted that four systematically replicated plots greatly reduces the error which arises from soil heterogeneity. The data also show that four systematically distributed plots of four trees each are somewhat more reliable than two plots of eight trees each.

As was presented in Chapter IV, Harris has given a reliable means of estimating soil heterogeneity by the correlation between the neighboring plots of a field. The test was applied to an orange grove which appeared to have uniform soil conditions. The correlation between the yield of eight-tree plots as ultimate units and grouped combinations of four such adjacent plots was found to be: $r = +0.533 \pm 0.085$. This showed a pronounced heterogeneity in the soil of this orchard. However, the correlation computed between the yield of an eight-tree ultimate unit and the yield of the combination of four such systematically distributed units was not much larger than the probable error.

These facts show the unreliability of yields of single trees as a criterion of productivity, that eight-tree plots give much more reliable results, and that plot replication is of as much value in studies of fruit-yield as of farm crops. Where quality is a major criterion, single trees give fairly reliable information.

Self-sterility and Heterozygosity.—One of the chief difficulties of systematizing methods of work is due to the heterozyogus

condition of most fruit material. A commercial variety may be extremely valuable and yet be heterozygous for many characters. On the other hand, the commercial variety may be homozygous for a large part of its characters. It seems reasonable to conclude that the more nearly homozygous the parental variety, other things being equal, the greater value it would have as a parent.

The ability of impressing its characteristics upon the larger part of its offspring has been called prepotency by animal breeders. Such prepotency is genetically explained by the supposition that the prepotent parent is homozygous for certain dominant factors for the characters under observation. Hedrick and Wellington (1912) showed that some crosses between apple varieties produced a considerable percentage of individuals with small fruits. Thus the cross between Ralls and Northern Spy gave great variability in size of apples, while the cross between Sutton and Northern Spy gave progeny in which no trees were obtained which produced small fruit. One of the great difficulties is that it takes several years to learn the varieties which when crossed will give certain desired combination.

Another difficulty which must be considered is that many varieties of fruits are self-sterile. This is of utmost importance in commercial fruit production for it is necessary to interplant such a variety with some variety which produces an abundance of pollen which is capable of fertilizing the variety in question and

TABLE LXXI.—INCREASE IN WEIGHT OF SEED AND FRUIT DUE TO CROSS-POLLINATION

Pollination	Average weight of seed, grams.	Average weight of fruit, grams.
Newtown × self	0.05	73
Newtown × Bellflower	0.40	104
Newtown × Spitzenberg	0.66	147
Newtown × Jonathan	0.65	162
Newtown × Grimes Golden	0.60	173
Spitzenberg × self	0.13	100
Spitzenberg × Newtown	0.65	126
Spitzenberg × Arkansas Blk	0.68	128
Spitzenberg × Jonathan	0.70	144
Spitzenberg × Baldwin	0.71	157

which blooms at about the same period. The self-sterile habit likewise prohibits the reduction of the material to a homozygous condition. Frequently self-fertile varieties give great increases in weight of seed and fruits as a result of cross-pollination. Therefore, pollinators, varieties which have proved desirable as pollen parents, are often of considerable commercial value in increasing yield in the case of self-fertile varieties.

Table LXXI gives two typical cases taken from the work of Lewis and Vincent (1909) with the apple.

The large increases in weight of seed as a result of crossing are

TABLE LXXII.—CONDENSED STATEMENT OF NUMBER OF SELF-FERTILE, SELF-STERILE, AND PARTIALLY SELF-FERTILE VARIETIES OF FRUIT CROPS

Fruit	Number self-fertile	Number self-sterile	Number partially self-sterile	Authority	Remarks
Grape.....	7	13	5	Dorsey, 1914 after Beach (1898, 1899)	Self-fertile and partially self-fertile have upright stamens and pollen with germ pore. Self-sterile varieties have reflexed stamens and pollen with no germ pore.
Grape.....	..	..	..	Beach, 1902	Pollen of self-sterile varieties can not fertilize other self-sterile varieties.
Plum.....	All cultivated varieties of native American species except New Ulm and Robinson are self-sterile.			Dorsey, 1919	Results given by Dorsey are from studies of Waugh (1896, 1897, 1898, 1899, 1900, 1901) Goff (1894, 1901), and Waite (1905).
Plum.....	18	16	5	Sutton, 1918	All self-sterile varieties set fruit when pollinated with any other variety with few exceptions.
Cherries...	3	17	2	Sutton, 1918	
Apples....	8	16	10	Sutton, 1918	
Apples....	28	59	..	Lewis and Vincent, 1909	From 50 to 200 pollinations were made for each variety. If no seed set, variety is classed as self-sterile. All varieties with some seed setting are classed as self-fertile, although some are partially self-sterile.
Pears.....	Bartlett and Kieffer pears are self-sterile.			Fletcher, 1911	

very noticeable. Increases in size of fruit are also of much importance.

For the commercial grower or the fruit breeder, it is essential to know which varieties are self-sterile. In order to illustrate the conditions generally found regarding sterility, a compilation of some results is presented in Table LXXII. Citations to literature are given so that the reader may go to the original sources when he desires to know what category any particular variety belongs to.

The causes of sterility have been determined in some cases. In the strawberry it is due to at least two causes (Valleau, 1918):

1. The diœcious condition.
2. The production of aborted pollen grains or microspores in otherwise normal anthers.

In the grape, Dorsey (1914) has found sterility to be associated with both hybridity and the dioecious condition. The varieties which produce reflexed stamens seldom produce fertile pollen. Dorsey states that:

> "Sterility has been found to be due to the pollen rather than in the pistil. Sterile pollen in the grape results from degeneration processes in the generative nucleus or arrested development previous to mitosis in the microspore nucleus."

Pollen abortion occurs both in pure and hybrid forms but is not considered a cause of lack of fertility as abundant pollen is produced in the grape.

In the plum, pollen abortion is not as a rule the cause of self-sterility. The outstanding features as given by Dorsey (1919) are:

> "(*a*) A constancy of expression of self-sterility even in *P. domestica* in which about one-half of the varieties are self-fertile; (*b*) the occurrence of cross-sterility; and (*c*) the slow growth of pollen tubes under the condition of self- and cross-sterility."

This type of sterility is comparable with that in the tobacco crosses previously discussed, where sterility resulted from slow pollen tube growth. In this case the pollen tube growing from the pollen grain into the tissues of the style never reaches the embryo sac. The self-sterile condition is believed by Dorsey to be a dominant character in the plum and to be inherited, segregation into sterile and fertile forms occurring at reduction division.

Knight (1917) has made a study of self-sterility in the apple and the conclusions reached show the manifold causes which must be considered in a study of the problem. For this reason the conclusions are here given verbatim.

"1. Self-sterility in Rome Beauty is not due to sterility of the pollen as has been shown to be the case in certain varieties of grapes.

"2. Sensitiveness of pollen to over-abundant moisture supply is not involved here as a factor, as has been shown by Jost for the pollen of many grasses, barley especially; and by J. N. Martin for the pollen of red clover. The pollen of Rome Beauty and many other varieties germinated in distilled water.

"3. Rome Beauty stigmatic fluid extracts offer no inhibition to the germination and growth of Rome Beauty pollen.

"4. Rome Beauty stigmas offer no particular mechanical obstruction to the penetration of Rome Beauty pollen tubes.

"5. Self-sterility of Rome Beauty is not due to inability of its own pollen tubes to grow deep enough to reach the egg. This has been suggested as the cause of self-sterility in certain pear and apple varieties by the work of Osterwalder.

"6. From present indications one important factor in self-sterility of Rome Beauty is the relatively slow rate of growth of Rome Beauty tubes in Rome Beauty stylar tissue. Doubtless other factors will be found upon further examination."

Inheritance of Some Characters.—The mode of inheritance of most fruit characters has as yet not been determined. There are, however, numerous experiments under way for the purpose of learning how individual characters behave in crosses. The lack of information in this field is due to the heterozygous condition of many fruit varieties and to the fact that with many fruit crops so long a period elapses between the time of sowing the seed and the production of fruit.

Apple.—Inheritance in the apple is well illustrated by a study made at the Geneva Station by Hedrick and Wellington (1912). Crosses were made in 1898 and 1899 and 148 seedlings were grown. In 1912, 106 of the seedlings had come into bearing. These 106 seedlings resulted from 11 crosses. The first generation naturally does not furnish very reliable data as a means of deciding the mode of inheritance of individual characters.

Three types of skin color were studied, red, yellow, and intermediates. The conclusion was reached that Ben Davis and Jonathan were both pure for red color of skin, as crosses between

these varieties gave seedlings which produced fruit with a red skin. Other crosses led to the belief that yellow is recessive and that a cross between red and yellow is intermediate in skin color. Sweetness was believed to be a recessive character to acidity with the indication that the F_1 was intermediate.

Raspberry.—Bailey (1898) believed that the purple raspberry, *Rubus neglectus,* was a natural hybrid between the black and red varieties. This was definitely proved at the Geneva Station by a cross between Smith No. 1, a black raspberry, and Lonboro, a red seedling, which gave 209 purple raspberries (Wellington, 1913, Anthony and Hedrick, 1916). The same Smith No. 1 crossed with June, a red raspberry, gave 50 purples and 46 blacks. Selfed seedlings of Columbian, a purple variety, gave 31 purple, 7 red wine, 2 reddish, 1 yellow, and 1 black. The mode of inheritance of colors can not be determined, although it seems that several of the black varieties are heterozygous for color and that several factors for color are present. The presence of bloom on the canes proved to be a partially dominant character over the absence of bloom. The number of spines on canes showed segregation in selfed seedlings of Columbian. Yellow raspberries could be told in the seedling stage from the black and purple by the absence of red tinge on the leaves. The production of promising varieties from crosses between the red and black varieties was especially mentioned.

Grape.—The Geneva Experiment Station, in New York, (Hedrick and Anthony 1915) likewise furnished the greater part of our data on inheritance of characters in the grape. Table LXXIII gives the results of crosses for skin color.

TABLE LXXIII.—INHERITANCE OF SKIN COLOR IN GRAPES

Color of parental types	Color of seedlings			
	Black	Purple to dark red	Medium to light red	White
White × white	...	..	..	166
Light red × light red	8	6	13	8
Dark red × dark red	38	43	45	42
Black × black	407	49	13	54
White × dark red	5	44	14	50
White × black	41	3	3	12
Black × dark red	100	52	40	32

The chief conclusions which may be reached from these results are that nearly all varieties are heterozygous for color and that white is a pure recessive.

In studies of inheritance of quality there is a proof of the value of selecting as parents the types which excel for the character being worked with. Table LXXIV gives some of the results of crosses in which quality was studied.

TABLE LXXIV.—INHERITANCE OF QUALITY IN THE GRAPE

Parental types	Total	Percentage of good or better
Parents good or of higher quality	682	27
Good × fair or poor	56	11
Medium × medium	213	10
Poor × poor	51	4

Nearly all grapes of high quality at the New York station contain some *V. vinifera* blood. This is easily understood when one remembers the long period of breeding of the European varieties and that American varieties were only recently obtained from the wild. Inheritance of size of grape berry and ripening period showed the value of selecting as parents varieties which excel in the character which the breeder wishes to obtain.

Illustrations of Methods of Breeding.—Methods of breeding fall naturally under three main heads;

1. Selection of bud sports.
2. Seedling selection.
3. Controlled crosses.

As has been already mentioned many of our varieties have resulted from chance seedlings, others from seedlings in which only one parent was known. A review of the subject leads to the conclusion that the improvement of fruits by the use of self-fertilized seed is a less desirable method than by the use of crossed seed. When selfed seed can be produced the progeny are as a rule less vigorous than those obtained from crossed seed. As these subjects have been touched upon in some detail under other headings, seedling selection will not be discussed further.

Selection of Bud Sports.—It is now a commonly accepted fact that mutations or sudden changes in the germinal material do occasionally occur. Likewise, in asexually propagated species

bud sports have been found, and in some cases these have been used as the foundation of improved races. To justify a method of breeding founded upon their utilization, such bud sports must occur frequently enough to pay for the trouble of making a systematic search for them.

A review of the experimental evidence is of considerable interest, for this is the only means we have of deciding whether the selection of particular trees or branches for propagating purposes is a reliable means of producing new varieties. Of the four apple bud sports mentioned in Table LXVIII the chief changes were in the color of the fruits. In the Isabella grape several sports were obtained which produced black grapes of larger size than Isabella, and which excelled in sweetness (Powell, 1898 cited from Dorsey, 1916). Dorsey (1916) records two large-fruited variations in the Concord grape which arose as bud sports.

Instances of bud variations in ornamental horticultural plants are quite common. As an example of their frequency, the work of Stout (1915) will be briefly discussed. Extensive asexual or clonal selections were made in *Coleus* and numerous color changes were isolated as well as changes in leaf shape. The same variations were obtained through bud sports as by seed reproduction. Some clonal lines sported much less frequently than others.

The work on citrus fruits (Shamel and others, 1918) which has been carried on in California, has drawn the attention of many horticulturists and plant breeders to the subject of bud sports and their place in correct fruit-breeding methods. Valencia oranges were originally introduced from three sources, but all have proved of similar type and are now called Valencia. From this variety 12 important strains originating as bud sports have been isolated. As a rule, single off-type branches produce fruits showing characters which are different from the fruits borne on the remainder of the tree. Many of these sports are of highly undesirable type. The Washington navel orange was introduced from Brazil in 1870 by the Department of Agriculture at Washington. Thirteen distinct strains have been isolated through bud selection. Thompson, one of these strains, has proved a very desirable type. Likewise, bud sports have occurred in the grapefruit which was introduced in California from Florida in 1890. The Marsh is the best of six strains which were obtained by selecting bud sports. Similarly bud sports have occurred in lemon orchards. Shamel (1919) records an occurrence of a sporting branch in a

French prune tree which was first observed in 1904. Several grafts from this branch were placed in bearing trees. These grafts reproduced the characters of the sporting branch. In 1914, trees in alternate rows of an orchard were top-worked by the use of buds from the new strain and compared with buds from the normal French prune variety. The top-worked trees from the bud sport bore larger fruit than those from the normal prune. The fruits were also more evenly distributed over the tree than in the original French prune variety.

The above are some of the more striking instances of the production of new varieties through the isolation of bud sports. Crandall (1918) has made an extensive test in Illinois of the value of bud selection in apples as a means of improving the variety. Two distinct lines of study have been followed.

1. The value for propagating purposes of buds selected in different ways. The experiments included a comparison of large *versus* small buds, of buds from different parts of the tree and from different locations on the shoot.

2. Selection of trees because of special merit. Comparison of seedlings produced from large and small apples produced by these selected trees.

A considerable number of varieties was used for the first study and a total of 5,400 buds were selected. A careful measurement was then made of the yearly growth of wood from the buds which had been previously selected. Growth curves were made and on the basis of these results the conclusion was reached that all buds from healthy shoots were of equal value for propagation purposes.

The characters of seedlings grown from seeds of large and small fruits borne on trees of special merit were carefully studied. Seeds from large fruits produced seedlings which were somewhat more resistant to adverse conditions than seedlings grown from small fruits. The hypothesis that this may be explained by the fact that large fruits and large seeds frequently occur from crosses, seems reasonable in the light of the work of Lewis and Vincent previously cited.

Stewart (1912) has discussed the value of cion selection in tree-fruit improvement. Individual apple tree data over a period of from ten to fourteen years were presented. Under apparently the same conditions some trees were consistently higher yielders than others. A review of considerable experimental evidence led

Stewart to conclude that there was more evidence in favor of purity of the clone than in favor of the value of clonal selection as a means of producing higher-yielding strains. Similar conclusions were reached from an experiment carried on by Tyson brothers, in New York, with the York Imperial apple. Two trees were selected which bore unusually similar fruits and these were used for propagation. More than 8,000 trees were planted in the new orchard. Examination of trees of this orchard when they came into bearing showed them to be not superior to the usual York Imperial apple (Dorsey, 1917).

The cited cases show the present status of the problem of selection of bud sports as a means of improvement of fruit crops. The studies with the citrus genus appear to justify the belief that degenerate or inferior bud sports are of frequent occurrence. This leads to a conclusion that only those limbs which produce normally healthy fruit should be used for propagation purposes. Even among the citrus fruits there is as yet no very conclusive proof that the selection of cions from high-yielding trees will accomplish more than to prevent possible "running out" of the variety. The evidence from apples would seem to justify the belief that bud sports are very infrequent. The breeder, then, can well afford to make careful observations with the hope of discovering bud sports. If apparently desirable sports are found, these may then be used for propagation.

In such crops as citrus fruits and with such plants as *Coleus*, bud sports are of frequent occurrence. There is, then, some evidence for the belief that sports occur more frequently in heterozygous than in homozygous material. As Stout (1915) obtained the same changes through asexual selection as by the use of self-fertilized seed, it seems reasonable to suppose that some sort of segregation and recombination occurs in somatic tissue. No cytological evidence has been given to account for such a supposition. With heterozygous material the loss of a single dominant factor would be immediately apparent in the soma. This is one reason why bud sports occur more frequently in heterozygous forms (East and Jones, 1919). Nabours (1919) has shown that similar cross-overs occur in parthenogenetic reproduction in the grouse locust as in those forms which are produced by the recombination of gametes containing the haploid number of chromosomes. If the usual sort of cross-overs occurred in homozygous material, there would be no change in the homologous parts of

chromosome pairs. In heterozygous material, however, new combinations of factors would be produced which might cause changes in the external appearance of the organism. No cytological basis for such cross-overs has been demonstrated.

Controlled Crosses.—One of the earliest controlled experiments in the breeding of fruits by crossing was started by Swingle, in 1893, in Florida. This was an attempt to produce hardier types by the use of wild citrus species. The hardy Chinese species, *Citrus trifoliata*, was used as one of the parents. In 1897, 212 crosses were made between this species and orange varieties. The three fruits that were produced gave thirteen hybrids, which were so different from existing varieties of citrous fruits that they were called "Citranges." Other crosses between citrous species were made. One of the promising combinations was a cross between the West India lime and the kumquat orange. This orange is one of the hardiest of the evergreen citrous trees while the lime is very tender. Further experiments are under way and other promising wild relatives of the citrous fruits have been obtained. Crosses of this nature are producing fruit varieties which are successful in regions where citrous fruits could not be grown formerly. The work shows the necessity of a thorough botanical knowledge of the wild relatives of the crop which it is hoped to improve by breeding.

A somewhat similar method of work with the hope of producing hardy apples for the Canadian Northwest was started by William Saunders in Canada in 1888. The wild Siberian crab, *Pyrus baccata*, which proved hardy on the prairies and withstood temperatures of 50° below zero, was used as the female parent and crossed with commercial apple varieties. Macoun (1915) states that the fruit of *Pyrus baccata* averages ½ in. in diameter and is quite astringent. The fruits obtained from some of the more promising of the crosses were not so large as desired, although some compared very favorably in size with ordinary crabs. They were of good flavor and proved hardier than any varieties of apples and crabs that had been tested up to that time. Several are here listed.

Jewel,	*P. baccata* × Yellow Transparent.	Size 1.4 by 1.3 in.
Columbia,	*P. baccata* × Broad Green.	Size 1.8 by 1.6 in.
Charles,	*P. baccata* × Tetofsky.	Size 1.6 by 1.5 in.

Recrosses between the best of these and apple varieties were

made and 407 trees were grown. Some varieties were obtained with larger fruits but these as yet have not been thoroughly tested for hardiness.

Pears have been frequently tried in the Dakotas but have failed for two causes (Hansen, 1915): (1) Lack of hardiness; (2) susceptibility to blight. The Chinese sandpear, *Pyrus*



FIG. 64.—Wolf, a hardy variety of plums which lacks quality of fruit. (*Photo loaned by Dorsey.*)

sinensis Lindley, obtained from Dr. Sargent, of the Arnold Arboretum, proved perfectly hardy and resistant to blight. Various crosses between this species and cultivated pears belonging to *Pyrus communis* have been made. Preliminary tests have shown that some of the seedlings were blight resistant and hardy. These results indicate that the problem of producing



FIG. 65.—Burbank, a plum of high quality produced by Luther Burbank. It lacks hardiness when grown in Minnesota. (*Photo loaned by Dorsey.*)

pears for the Northwest may eventually be solved. In a somewhat analogous manner, Hansen (1911) has produced new plum varieties by crossing the native sand cherry with Japanese plums. This has resulted in a "happy combination of hardiness, rapid growth and early bearing of tree, with large size and choice quality of fruit."

It will be of interest here to present briefly an instance from the fruit-breeding work at the Minnesota Station in which desirable new plum hybrids were obtained when the tender parent, Burbank (*P. triflora*) was crossed with Wolf which is a hardy variety of *P. americana mollis*. The percentage of hybrids killed during winter dormancy is taken as a basis for classification. It will be seen that some of these hybrids, as No. 8 or No. 9, are hardy in the bud like the staminate parent Wolf. The two which have been named Red Wing and Tonka, are intermediate in hardiness but of excellent fruit characteristics.

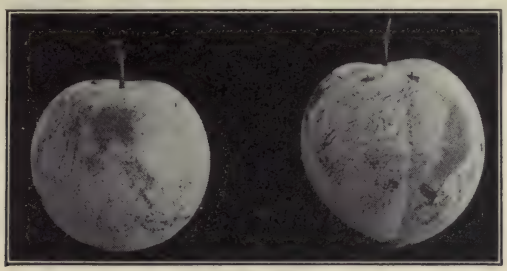


FIG. 66.—Tonka, Burbank × Wolf, No. 21. Has high quality and is nearly as hardy as the hardy variety of Wolf. (*Photo loaned by Dorsey.*)

TABLE LXXV.—SHOWING THE PERCENTAGE OF BUDS KILLED IN AN F_1 PROGENY WHEN ONE OF THE PARENTS IS HARDY AND THE OTHER TENDER[1]

Parent	Percentage of buds killed 1916–17	Parent	Percentage of buds killed 1917–18
Burbank	100	Hybrid No. 9	0
Wolf	0	10	50
Hybrid No. 1	50	11	1
2	35	12 (Red Wing)	10
3	5	14	25
4	5	15	5
5	10	16	5
6	10	17	0
7	0	20	25
8	0	21 (Tonka)	25

These few instances have been given as indicative of the methods of work which are being used by some of the most progressive fruit breeders. Some general conclusions regarding methods of work may be here given.

[1] Data furnished by M. J. Dorsey.

1. A knowledge of the botanical relationship and wild relatives of the fruit are necessary if greatest progress in improvement is to be obtained.

2. Some varieties and species transmit their characters to a much greater degree than do other varieties. A knowledge of the more prepotent varieties materially aids in planning a cross.

3. Varieties selected as parents should contain in the highest degree possible the character or characters desired in the progeny.

4. The larger the numbers of progeny grown, the greater the chances of obtaining the combination desired.

5. Most fruit crosses give variable progeny in F_1. Numerous crosses should, therefore, be made.

6. Information regarding the mode of inheritance of particular characters will assist in selection of varieties to be used as parents.

CHAPTER XIX

FARMERS' METHODS OF PRODUCING PURE SEEDS

The production of new varieties of farm crops is a specialized line of work and should be undertaken as a rule only by men who have had special training in crop breeding. The expense and time necessary for this kind of experimental work are too great for the individual farmer. The aim of the farmer or seed grower should be to maintain the improved form and not to allow contamination through crossing with inferior stock, admixture, plant diseases, etc. A method of producing seed which will stand this test and at the same time meet with the approval of the farmer must be simple, effective, and inexpensive. A nation or state cannot afford to maintain an experimental laboratory only to have the products of that laboratory deteriorate because of subsequent treatment. The maintenance of pure, improved varieties as well as their discovery by selection or synthesis by crossing is an essential factor in economic food production. Before taking up in detail methods of producing pedigreed seed by farmers, a few observations regarding seeds in general will be made.

DETERMINATION OF BETTER VARIETIES

Certain general facts regarding varieties should be understood. The breeder and grower must recognize that no one variety is best adapted to a particular locality or for all seasons. In some seasons an early oat gives the best yield. Owing to slight seasonal variations, a later variety may excel in yield. Thus, a single season's test is not reliable as a means of determining the better sort to grow. For this reason carefully conducted tests are carried on each crop season. By means of these the experiment stations are in a position to determine and advise as to the better varieties. The final decision as to which variety to grow must of course be made by the farmers and based on their actual field experiences.

WHAT IS GOOD SEED?

There are certain characters of farm crops which must be considered if the grower wishes to produce good seed. Good seed of any farm crop must belong to a variety that is superior in the following respects:

1. Adaptability to the locality and soil.
2. Yielding ability.
3. Purity to type for small grains or self-pollinated crops, and comparative purity for corn and other cross-pollinated crops.
4. Quality for the particular characters for which the crop is grown.
5. Hardiness.
6. Erectness or ability to withstand lodging.
7. Disease escaping or resistance to disease.

The seed of the particular variety itself must be superior in the following:

1. Germinating ability.
2. Good color, plumpness and weight.
3. Uniformity.
4. Freedom from diseases transmitted by seed.
5. Freedom from any other damage.
6. Freedom from obnoxious weeds.
7. Freedom from mixture with other varieties.

Adaptability.—We have already indicated that no one variety always excels in yield or quality. All that the experiment stations can do is to determine the few better varieties and in this way assist the farmer to decide which to grow.

There are decided advantages in limiting the number of varieties. It is of considerable value for one locality to produce large quantities of a particular variety. Several reasons are apparent, chief of which are: (1) The buyer can obtain a large amount of seed of that particular variety. (2) The production of only a few varieties or a single variety is of material help in keeping purity of type, as there is not so much opportunity for (*a*) mixtures in thrashing, growing, etc., or (*b*) cross-fertilization between varieties, which causes variability of seed and plant characters and, therefore, loss of purity of type.

Yielding Ability and Quality.—Variety tests carried on under experimentally controlled conditions are the best means of determining comparative yield and to some extent comparative quality

of different strains. Many farmers sustain annual losses, which are not small, due to using seed of an over-exploited variety which has not proved its worth in competitive tests. With many crops, quality is of prime importance and must receive some consideration if a No. 1 grade product is to be obtained.

Purity.—For crops like wheat, oats, and barley, which are self-fertilized, uniformity is the rule, providing the grower is willing to pay some attention to eliminating accidental mixtures. For cross-fertilized crops, of which corn is a good example, purity of type is of less importance, although certain general standards of purity are desirable.

Hardiness.—Hardiness is a feature of adaptability but it deserves especial mention. Ability of annual crops like rye and wheat to withstand winter-killing as well as winter hardiness for perennial crops such as alfalfa is of high importance and is generally given much consideration by experimenters before recommending a particular variety.

Strength of Stalk.—Ability to stand up, which obviates injury from lodging, is of much importance in grain and hay crops. In small grains early lodging often causes shriveled seeds. The difficulty of harvesting is greatly increased when the crop is flat.

Disease Escaping or Resistance.—Some varieties are much freer from disease than others. There are various factors, but the chief ones may be considered under disease escaping and disease resistance. Disease escaping may be due to early maturity, as in the case of Marquis wheat, which often escapes stem rust epidemics when late varieties such as Bluestem are seriously injured.

Disease resistance is the condition which obtains when the organism gains entrance to the plant yet causes no appreciable injury. There is, for example, a distinct tendency for *durum* wheat to be resistant to stem rust; some *durum* strains being much more resistant than others.

The above are some of the important agronomic or horticultural characters which separate one variety from another. By a knowledge of these the grower is enabled to obtain the best available strain for his conditions. Seed of this selected variety must then be saved in such a manner that it will have germinating ability, *i.e.*, will grow vigorously. In order to do this the seed must be mature and well developed and free from transmissible diseases. Freedom from obnoxious weed seeds is also an important consideration.

METHODS OF SEED PRODUCTION

After obtaining the better variety for the locality, the seed grower has the problem of keeping this variety in the same high state of production and if possible to improve it. The purpose of this chapter is to outline methods for the various crops which may be used by the seed grower or by the average farmer.

Farm crops may be placed in four groups according to their modes of reproduction. There is a close relation between this characteristic and the farmer's methods of seed production. The four groups mentioned are as follows:

Group 1.—Generally self-fertilized: Barley, wheat, oats, peas, beans, flax, tobacco.

Group 2.—Often cross-pollinated: Corn, rye, most grasses, root crops.

Group 3.—Cross-pollination obligatory: Red clover, sunflower.

Group 4.—Vegetatively propagated: Potatoes, sugar cane, sweet potatoes.

Among farm crops, the production of seed generally depends on a union of the male reproductive cell, contained in the pollen grain, with the female reproductive cell—the egg cell.

The pollen grains of corn are produced in the tassel and each thread of silk leads to an ovary which contains the egg cell. In order to produce seed, the male reproductive cell must pass down through the silk and unite with the female cell. This process is called fertilization. If pollen and silk are borne by the same plant the process is self-fertilization, and if by different plants, cross-fertilization. As the egg cell and the pollen grain of self-fertilized plants are, as a rule, alike in their inherited characteristics, the progeny of a single self-fertilized plant, such as barley, wheat, or oats, have the same inheritance. There is, of course, considerable variation in all characters, owing to environmental effect, but all evidence shows that these differences are not truly inherited. Occasional crosses occur in self-fertilized crops which cause inheritable variability. Mass selection serves to eliminate these off types.

SEED GROWERS METHODS FOR SELF-FERTILIZED PLANTS

For self-fertilized plants the grower can, as a rule, obtain a pedigreed strain which is nearly adapted to his conditions. The only thing that he can do with this variety is to save seed in such a way that mixtures of other strains or occasional crosses are eliminated, together with obnoxious weed seeds and diseases.

The strain in question can be kept in a pure condition for its characters, and if it is not entirely pure at the outset a correct method of seed selection will tend to purify it and thus to increase its value. The work for self-fertilized crops is very simple as compared with the production of improved seed of cross-fertilized crops or the production of highly bred livestock. For self-fertilized crops the method outlined is essentially that which is compulsory for the production of registered seed by the Canadian Seed Growers' Association.

The steps are given here with the understanding that the grower has already obtained the best available variety for his soil and climatic conditions. The chief points are as follows:

1. The use of a yearly hand-selected seed plot of at least ¼ acre in size, in a good state of cultivation, free from weeds, under a proper rotation, and sown at the regular rate of seeding.

2. The hand selection from this plot of enough seed of uniform character, thoroughly mature and free from disease, to plant the following year's seed plot. This selection may be accomplished before the plot is harvested or from the shock before thrashing.

3. The selected heads, panicles, or pods should be thrashed by hand and the seed carefully stored.

4. The removal of all impurities, weed seeds or mixtures of other varieties, from the seed plot before it is harvested. *Purity of seed is important.*

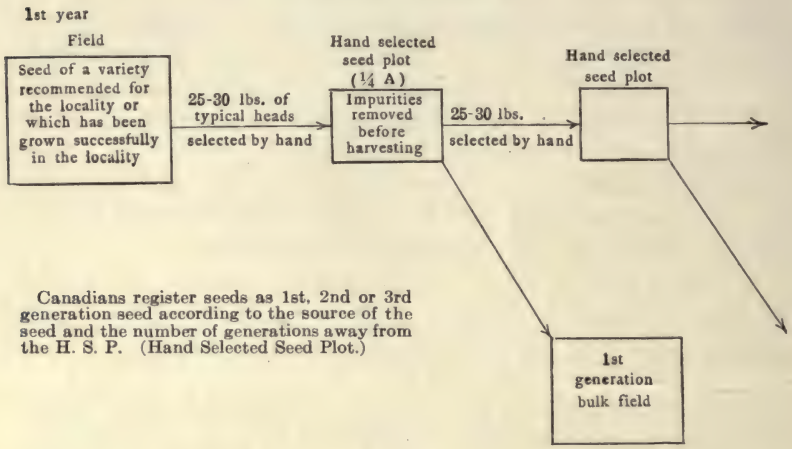
5. The bulk crop on the seed plot should be allowed to mature thoroughly, should be harvested carefully, and used the following year to sow as much of the bulk field as possible.

According to plans adopted by the Canadian Seed Growers' Association, seed may be registered which is not more than three generations away from the hand-selected seed plot. Such seed is inspected in the field and after being thrashed, and must conform to certain standards of purity and freedom from diseases.

The seed plot method is of particular interest to farmers for grain crops—barley, wheat, and oats. It could be used to advantage for flax, beans, and possibly peas, although in the case of peas the selection of seed would be somewhat more difficult. For these crops there seems to be no good reason why the seed plot could not be a part of the main field, *although the grower must not forget that the seed plot needs some extra attention if the work is to be worth while.*

The seed plot method is here outlined by means of a diagram.

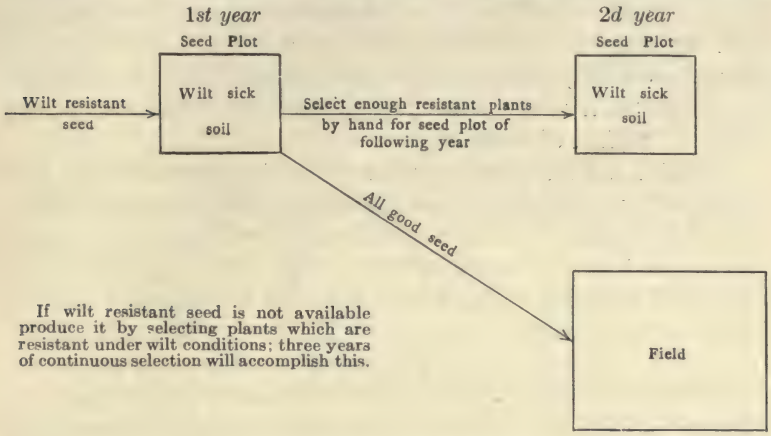
DIAGRAM OF FARMER'S METHOD OF MAINTAINING THE PURITY OF SELF FERTILIZED CROPS



For the tobacco crop there is no necessity of a seed plot. The grower should select good-type plants in the field and save these for seed production. The best growers insure the production of self-fertilized seed by covering the inflorescence before any of the flowers open, with a 12-lb. manila paper bag. It is necessary to remove the bag from time to time to shake out the dead parts of the corolla so that the seed will not become damaged. Ten or twelve plants handled in this manner furnish sufficient seed for a large acreage.

If the farmer is troubled with flax wilt he can easily overcome this difficulty by seed selection. All that is necessary is to select from a plot on which the wilt disease is causing considerable loss those plants which appear to be free from the disease. Experiments carried on by Bolley at the North Dakota Station which have been recently corroborated (Stakman *et al*, 1919), have shown that a wilt-resistant type can be produced by three years of continuous selection. Methods of producing wilt resistant seed are presented here in diagrammatical form:—

DIAGRAM OF METHOD OF CONTROLLING FLAX WILT BY SELECTION



IMPROVED CORN SEED

The determination of the better variety of corn to grow is not difficult. The farmer can obtain reliable advice from the local county agent or by consulting the nearest experiment station. The introduction of new varieties of corn from other states before they have been tested for the climatic conditions in question is a very undesirable practice and as a rule a cause of much annual loss to the corn grower. The problem with corn is somewhat different from that with the self-fertilized crops. Corn is cross-fertilized, therefore constant inherited variability is the rule. When a variety is introduced from another locality it undergoes a process of selection which may markedly change its characters. Selection in a pedigreed line of wheat, on the contrary, does not change its characters and serves only to keep the variety in the same state of purity by artificially removing any possible mixtures which may occur. This brief discussion will probably serve to show that seed selection on the farm is a very important practice for the corn grower, unless there is a local grower of high grade seed.

The corn seed grower faces another difficulty which the small-grain seed producer does not have to consider. With small grains—barley, oats, and wheat—purity for all characters is the general rule. This has led the corn breeder also to attempt to obtain purity of type. Carefully controlled investigations have served to show a possible fallacy in this practice. The

report of a recent study at the Minnesota Station (Olson, Bull, and Hayes, 1918), which contains experimental evidence together with a review of other experiments in relation to score card characters and yield, show no correlations between individual characters such as trueness to the ideal score card ear type and subsequent yield of these ears.

Artificial self-fertilization in corn isolates homozygous types which are less vigorous than normally cross-pollinated plants. All other evidence seems to show that too close a purity of type corn tends to a reduction in vigor. The grower whose method of selection is based upon ear type is certainly obtaining no gain in yield of shelled corn per acre. The detrimental results of too close selection to type may not be very apparent and may be more than counterbalanced by the extra attention from a cultural standpoint, for an interest in ideal ear types certainly stimulates the farmer to produce better corn. It is not, however an increase due to better breeding but to better cultural practice.

The present purpose is to outline methods of seed selection. As there is no apparent relation between score card characters for type of ear planted (within a particular variety) and resultant yield, even though such selection may be constantly practiced, we may pay little attention to those characters as far as our breeding plan goes. The grower should, of course, produce corn of one variety which is pure, judged by easily evident characters, such as color of seed and cob. Abnormalities, such as very large butts, badly flattened cobs, or very irregularly rowed ears, should not be used as foundation stock. Aside from these there is no need of paying much attention to type. Ability of a variety to mature under the conditions, is very important and needs much attention.

Two methods of work are outlined here, either of which may be of considerable value in increasing yield.

METHOD OF BREEDING CORN FOR SPECIAL BREEDERS

Nearly all discussions of corn breeding are based on the ear-to-row method. Such a method takes considerable time and can be carried out only by the breeder or occasional seed specialist. The ear-to row test is commonly understood. It consists of growing the seed of a certain number of ears in individual rows and determining the better yielding ones. Each ear saved is

then a basis of further selection. Complicated methods have been used for the introduction of new blood and to keep up the vigor of the strain. The method here outlined is an attempt to simplify this practice and at the same time obtain as good results as can be obtained by the more detailed procedures. It is based on experimental studies carried on at the Nebraska Station (Montgomery, 1909). The details are as follows:

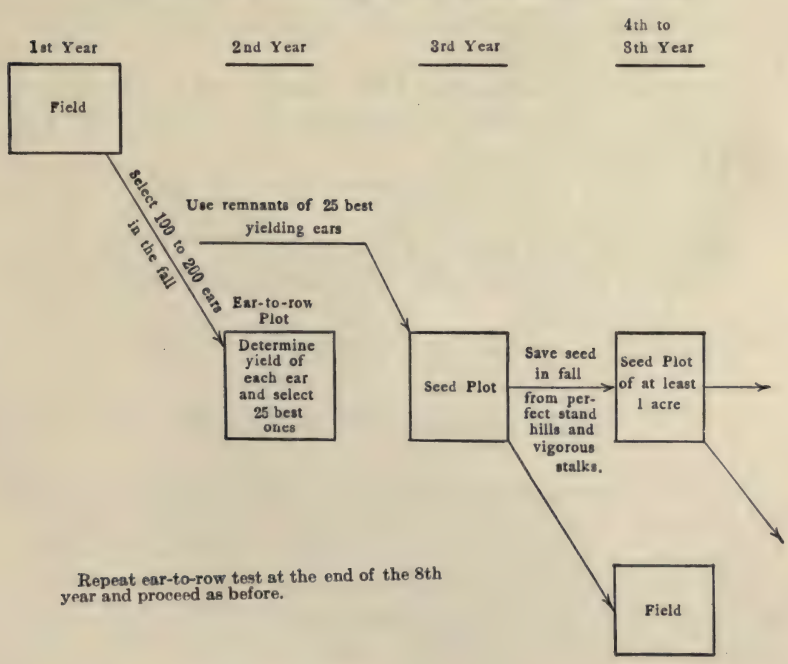
1. Select from 100 to 200 ears of the variety to be grown. If possible, select these ears in the field from those stalks which if in a perfect stand will give a good yield.

2. Make an ear-to-row test of these selected ears, saving half of the seed from each ear planted. From this ear-to-row test the 25 best ears may be determined.

3. Mix the remnants of the 25 highest yielding ears and plant the following year in a seed plot. Select all ears obtained which are fairly desirable, eliminating only the very undesirable types.

4. Use the selected seed for planting as much of the corn acreage as possible.

DIAGRAM OF PROCEDURE FOR SPECIAL CORN BREEDER



5. Give special attention to a part of the field so that a uniform stand may be obtained. Select enough seed from this part of the field for the entire acreage. Select seed for the following year's seed plot in the fall before a killing frost, from perfect stand hills and from those stalks which appear free from disease and which under competition show ability to produce one or more good ears. Throw away only the ears of very undesirable type.

6. Continue the method outlined under 5 for a period of four or five years and then use again the ear-to-row method as outlined under 1 and 2.

METHOD OF CORN BREEDING FOR AVERAGE FARMER

The average corn grower does not have time or facilities for accurate ear-to-row work. The method here outlined is very simple, yet is probably nearly as good for the average corn variety as the more complicated one previously given.

1. (*a*) Give special attention to a part of the field, or use a seed corn plot.

(*b*) Plant and cultivate carefully, using the hill method, and grow four stalks per hill.

(*c*) Each fall before frost select enough seed for the following year's seed plot from stalks which give a good yield and which grow in four-stalk hills.

(*d*) Discard only the very undesirable ears and store each selected ear in a careful manner.

(*e*) Test all seed used for germination.

2. Save all good seed produced by the yearly seed plot to plant the general field.

3. Continue 1 and 2 each crop season.

POTATO SEED (TUBERS) SELECTION

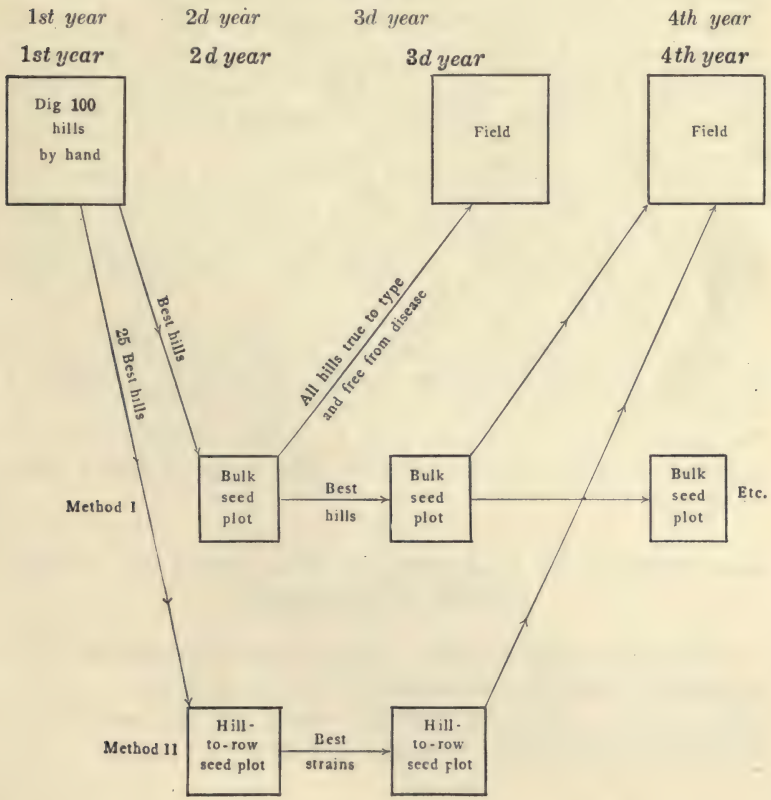
All localities are not equally good for producing potato tubers for planting, therefore it will be better for some farmers to buy tubers from a different locality. At University Farm, experiments of the Division of Horticulture show that tubers should be produced at some other locality if high yields are to be obtained. For the farmer, however, who lives in a locality where

desirable tubers for planting are produced, there are some methods which are of help to him in saving tubers.

Ordinarily the plants grown from tubers of a single plant are alike except for the occasional changes which occur in the inherited characters of the plant itself. Mixture in commercial tubers is one common cause of lack of purity of type. The selection of tubers, therefore, gives the grower an opportunity to improve his variety and also insures a constant supply of tubers free from diseases. This freedom from disease is a very important point (Tolaas and Bisby, 1919).

The first step of the grower is to obtain the best available variety, true to type and free from disease. After obtaining such a variety, one of the following plans may be followed. Both are alike for the first year's work.

DIAGRAMMATICAL ILLUSTRATION OF TUBER SEED PLOT SELECTION OF THE POTATO



First Year.—(*a*) Remove from the part of the field used for saving tubers all plants which show evidences of diseases. This should be done during the growing season.

(*b*) At harvest time dig at least 100 hills by hand, keeping each hill separate.

(*c*) Use tubers from a number of the better hills for the stock plot the following year.

Second Year.—Method I.—Plant all good tubers from previous year's selection of best hills in a bulk seed plot. Enough tubers should be used to plant about ¼ acre. This requires approximately 5 bushels, which allows some tubers to be discarded.

Method II.—This is the hill-to-row method. In order to compare the productive capacity of each selected hill it is desirable to have each row the same length and planted from the same total weight of potatoes. All of the progeny of some hills will be discarded this second year. Those that give a good yield and are desirable in other ways may be further tested.

Third Year. Method I.—Continue the stock plot by the same means as used in Method I for the second year's work, and use all good tubers produced each year in this seed plot for field planting. This work may be continued each succeeding season by the same plan.

Method II.—Make a further test of the best selections as determined by the second year's test, growing much longer rows, thus obtaining more reliable results. All tubers free from disease, of the best yielding strain or strains, may be used to increase the stock the following year.

The essential features of these two methods are presented on page 291 in diagrammatical form. Method II probably is somewhat better if all details of the test are carefully performed. For the average farmer, Method I is less cumbersome and if constantly practiced would probably give about as good a result as Method II.

IMPROVEMENT BY SELECTION OF SUCH CROPS AS ALFALFA, CLOVER, AND GRASSES

Obtain, if possible, a variety which is especially adapted to the conditions. Breeding work should aim at producing a variety which excels in resistance to winter injury and to plant diseases and is also a high producer of hay and seed.

The following is an outline of the possible steps:

1. Obtain 3 or 4 pounds of the best available seed.
2. Plant in a seed plot isolated as far as possible from other crops of a like kind. Plant seed in rows 3 ft. apart and plant two or three seeds in each hill, spacing the hills two ft. apart in the row.
3. Remove all but a single plant from each hill when the plants are well started.
4. Keep the plot free from weeds.
5. Discard all weak plants from time to time as they become apparent.
6. Save seed of all desirable plants and increase.

The improvement of the class of crops here mentioned is somewhat more difficult than with small grains, corn, and potatoes, and should be undertaken only by the few seed producers who are willing to take the necessary trouble to carry out carefully the details as outlined. Controlled experiments at some of the state experiment stations and in Europe have shown that much gain can be obtained by such selection.

SEED REGISTRY OR CERTIFICATION

The outlined seed plot methods are based upon fundamental breeding principles. In order to protect the seed grower who follows such a practice, some system of seed certification is advisable. Various methods have been developed by crop improvement associations. The details of procedure are those which are based upon fundamentally sound business practice. Seed that is eligible for registration must conform to certain standards of purity and freedom from plant pests. The seed-plot methods, if carefully followed, insure the production of seed of a certain standard grade. Certification or registration shows that the seed has been approved by the trained seed inspector.

DEFINITIONS[1]

Acquired Character.—A modification of bodily structure, function, or habit which is impressed on the organism in the course of individual life.

Aleurone.—The outermost layer of the endosperm in cereals, when it is rich in gluten.

Allelomorph.—One of a pair of contrasted characters which are alternative to each other in Mendelian inheritance. Often used, but with doubtful propriety, as a synonym for gene, factor, or determiner.

Allelomorphism.—A relation between two characters, such that the determiners of both do not enter the same gamete but are separated into sister gametes.

Alternative Inheritance.—A distribution of contrasting parental or ancestral characters among offspring or descendants, such that the individuals exhibit one or other of the characters in question, combinations or blends of these characters being absent or exceptional.

Anthesis.—The period or act of flowering.

Awn.—A bristle-shaped elongated appendage or extension, to a glume, akene, anther, etc.

Barbed.—Furnished with rigid points or short bristles, usually reflexed.

Biotype.—A group of individuals all of which have the same genotype.

Bran.—The coat of the caryopsis, consisting of pericarp and seed-coat united.

Caryopsis.—A one-seeded dry fruit with the thin pericarp adherent to the seed, as in most grasses.

Centgener.—Originally used by W. M. Hays, at the Minnesota Station, to refer to a 100-plant plot in which each seed was planted a certain distance from each other seed.

Chaff.—The floral parts of cereals, generally separated from the grain in thrashing or winnowing.

Chimera.—An association of tissues of different parental origin and genetic constitution in the same part of a plant.

Chromosome hypothesis.—The hypothesis advanced by Morgan in which factors are arranged in the chromosomes.

Class.—In genetics a group that includes variates of similar magnitude.

Clone.—A group of individuals produced from a single original individual by some process of asexual reproduction, such as division, budding, slipping, grafting, parthenogenesis (when unaccompanied by a reduction of the chromosomes), etc.

Coefficient of Variability.—A relative index of variation obtained by expressing the standard deviation in percentage of the mean.

Coupling.—Such a relation between the genes of two unit-characters that they have a more or less marked tendency to be included in the same gamete when the individual is heterozygous for both of the genes in question.

[1] Many of the genetic definitions are taken from Shull (1915), Babcock and Clausen (1918) or others. Ball and Piper's (1916) papers on terminology have been used for agronomical terms.

Cross.—Synonymous with hybrid.

Cross-fertilization.—The union of the egg cell of an individual with the sperm cell of a different individual whether the organisms belong to the same or different genotypes.

Cross-over.—A separation into different gametes, of determiners that are usually coupled, and the association of determiners in the same gamete which are generally in different gametes.

Detassel.—To remove the tassel, as in maize.

Cryptomere.—A factor or gene whose presence can not be inferred from an inspection of the individual, but whose existence can be demonstrated by means of suitable crosses.

Determiner.—Synonymous with gene or with factor as applied in genetics.

Dominance.—In Mendelian hybrids the capacity of a character which is derived from only one of the two generating gametes to develop to an extent nearly or quite equal to that exhibited by an individual which has derived the same character from both of the generating gametes. In the absence of dominance the given character of the hybrid usually presents a "blend" or intermediate condition between the two parents, but may present new features not found in either parent.

Dominant.—(1) A character which exhibits dominance, *i.e.*, that one of two contrasted parental characters which appears in the individuals of the first hybrid generation to the exclusion of the alternative "recessive" character. (2) An individual possessing a dominant character in contrast to those individuals which lack that character which are called "recessives."

Ear.—A large, dense or heavy spike or spikelike inflorescence as the ear of maize. Popularly applied also to the spike-like panicle of such grasses as wheat, barley, timothy and rye.

Emasculation.—The act of removing the anthers from a flower.

Endosperm.—The substance which surrounds the embryo in many seeds, as the starchy part of a kernel of wheat or corn.

Factor.—An independently inheritable element of the genotype whose presence makes possible a specific reaction or the development of a particular unit-character of the organism which possesses that genotype; a gene or determiner.

Floret.—A small flower, especially one of an inflorescence, as in grasses and Compositæ.

F_1, F_2, F_3, etc.—1st, 2nd, and 3rd, etc. generations following a cross.

Gamete.—A reproductive cell containing x number of chromosomes.

Gene.—Synonymous with determiner or factor.

Genotype.—The fundamental hereditary constitution or sum of all the genes of an organism.

Glabrous.—Smooth, especially without hairs.

Glume.—One of the two empty chaffy bracts at the base of each spikelet in grasses.

Grain.—Cereal seeds in bulk.

Group.—In genetics a broad general term for a complex of other categories and not for a complex of any particular category.

Head.—A dense, short cluster of sessile or nearly sessile flowers on a very short axis or receptacle, as in red clover or sunflower.

Heredity.—The distribution of genotypic elements of ancestors among the descendants; the resemblance of an organism to its parents and other ancestors with respect to genotypic constitution.

Heterozygosity.—The condition of an organism due to the fact that it is a heterozygote; the state of being heterozygous; the extent to which an individual is heterozygous.

Heterozygote.—A zygotic individual in which any given genetic factor has been derived from only one of the two generating gametes. Both eggs and sperms produced by such an individual are typically of two kinds, half of them containing the gene in question, the rest lacking this gene; consequently the offspring of heterozygotes usually consist of a diversity of individuals, some of which possess the corresponding character while others lack it.

Heterozygous.—The state or condition found in a heterozygote.

Heterosis.—The increased growth stimulus often exhibited in the F_1 generation of a cross.

Homozygosis.—The state of being homozygous; the extent to which an individual is homozygous.

Homozygote.—An individual in which any given genetic factor is doubly present, due usually to the fact that the two gametes which gave rise to this individual were alike with respect to the determiner in question. Such an individual, having been formed by the union of like gametes, in turn generally produces gametes of only one kind with respect to the given character, thus giving rise to offspring which are, in this regard, like the parents; in other words, homozygotes usually "breed true." A "positive" homozygote with respect to any character contains a pair of determiners for that character, while a "negative" homozygote lacks this pair of determiners.

Homozygous.—The state or condition found in a homozygote.

Hybrids.—The progeny of a cross-fertilization of parents belonging to different genotypes.

Hull.—A term applied to include the lemma and palea when they remain attached to the caryopsis after thrashing.

Hypostasis.—That relation of a gene in which its usual reaction fails to appear because of the masking or inhibitory effect of another gene; contrasted with "epistasis."

Inflorescence.—The flowering part of a plant.

Keel.—A central ridge resembling the keel of a boat, as in the glumes of some grasses, etc.; also the inferior petal in the legume flowers.

Kernel.—Matured body of an ovule; seed minus its coats.

Lethal.—A genetic condition causing death.

Linkage.—The type of inheritance in which the factors tend to remain together in the general process of segregation.

Lodicule.—A minute scale at the base of the ovary opposite the palea in grasses, usually two in number, and probably representing the reduced perianth.

Mean.—The arithmetical average.

Mode.—The class of greatest frequency.

Mendelize.—To follow Mendel's law of inheritance.

Multiple Allelomorphs.—Three or more characters which are so related that they are mutually allelomorphic in inheritance.

Mutant.—An individual possessing a genotypic character differing from that of its parent or those of its parents, and not derived from them by a normal process of segregation.

Mutate.—To undergo a change in genotypic character independently of normal segregation.

Ovule.—Female sex cell with its immediate surrounding parts.

Ovum.—Egg cell.

P_1, P_2, etc.—The 1st, 2nd, etc. generation of the parents.

Palea.—The upper of the two bracts immediately enclosing each floret in grasses.

Panicle.—A compound inflorescence with pediceled flowers usually loose and irregular, as in oats, rye, proso, etc.

Pedicel.—A stalk on which an individual blossom is borne.

Peduncle.—The primary stalk supporting either an inflorescence or a solitary flower. In grasses the uppermost internode of the culm.

Pericarp.—The matured wall of the ovary.

Phenotype.—The apparent type of an individual or group of individuals, *i.e.* the sum of the externally obvious characteristics which an individual possesses, or which a group of individuals possess in common; contrasted with genotype.

Presence and Absence Hypothesis.—The hypothesis that any simple Mendelian difference between individuals, results solely from the presence of a factor in the genotype of the one individual, which is absent from that of the other. Presence and absence of unit-differences as a convenient *method* of describing the results of genetic experiments should be carefully distinguished from the presence and absence hypothesis. The *method* is purely objective and entirely free from hypothetical implications.

Probable Error.—A measure of accuracy for results obtained by statistical methods. The chances are even that the true value lies within the limits marked by the probable error.

Probable Error of a Single Determination.—S. D. $\times \pm 0.6745$.

Probable Error of a Difference.—The square root of the sum of the squares of probable errors of the two results, or the probable error of a single determination multiplied by the $\sqrt{2}$.

Pubescent.—Hairy in a general sense; in special use, covered with short, soft hairs.

Pure Line.—A group of individuals derived solely by one or more self-fertilizations from a common homozygous ancestor. Sometimes erroneously applied to groups of individuals believed to be genotypically homogeneous (a homozygous biotype or a clone) without regard to the method of reproduction.

Recombination.—Union of parental factors in individuals of the second or later generations after a cross.

Reduction Division.—That in which homologous chromosomes separate preparatory to formation of gametes.

Repulsion.—Such a relation between two genetic factors that both are not, as a rule, included in the same gamete, referring especially to cases in which the factors in question give rise to obviously different characteristics; also called "spurious allelomorphism."

Replication.—Systematic repetition. Used in field work to designate the systematic distribution of plots of each strain or variety to overcome soil heterogeneity. Two replications means the use of three plots systematically distributed.

Roguing.—The act of removing undesirable individuals from a varietal mixture in the field by hand selection.

Seed.—The mature ovule, consisting of the kernel and its proper coat.

Self-fertilization.—The union of the egg cell of one individual with the sperm cell of the same individual.

Self-sterility.—That condition in which the male gametes of an organism are incapable of fertilizing the female gametes of the same individual.

Segregate.—With reference to Mendelian unit-characters, to become separated through the independent distribution of the genetic factors before or at the time of the formation of the gametes.

Sex-linked Inheritance.—The association of the determiner for any unit-character with a sex-determiner, in such a manner that the two determiners are either generally included in the same gamete, or that they are generally included in different gametes.

Somatic Segregation.—Segregation during somatic division.

Species.—A group of varieties or a single variety which in botanical characters and genetic relationship can be differentiated from another group or variety belonging to the same genus or to other genera.

Spikelet.—A small or secondary spike, especially in the inflorescence of grasses.

Spike.—A simple inflorescence with the flowers sessile or nearly so on a more or less elongated common axis or rachis.

Sperm or Sperm Cell.—Male sex-cell.

Standard Deviation.—An absolute measurement of variation in terms of the mean. The square root of the sum of the deviations squared divided by the number of variates.

Sterility.—Inability to reproduce; when male and female gametes, through incompatibility or some other cause, are incapable of mating or fertilization.

Strain.—A group within a variety which constantly differs in genetic factors or a single genetic factor difference from other strains of the same variety.

Tassel.—Used to designate the staminate inflorescence of maize.

Unit-character.—In Mendelian inheritance, a character or alternative difference of any kind, which is either present or absent, as a whole, in each individual, and which is capable of becoming associated in new combinations with other unit-characters.

Variate.—A single magnitude determination of a character.

Variety.—A group of strains or a single strain which by its structural or functional characters can be differentiated from another variety.

Variety Group.—A complex of varieties which resemble each other more than varieties belonging to a different group. Of lower grade than species.

Xenia.—The apparent immediate effect of pollen. It results from double fertilization.

Zygote.—The body formed by the union of two gametes and containing $2x$ number of chromosomes.

LITERATURE CITATIONS

AARONSOHN, A., 1910. Agricultural and botanical explorations in Palestine. U. S. Dept. Agr., Bur. Plant Indust., Bull. 180, 52 pp.

ALLARD, H. A., 1919*a*. Some studies in blossom color inheritance in tobacco, with special reference to N. sylvestris and N. tabacum. Am. Nat., **53**: 79–84.

1919*b*. Gigantism in Nicotiana tabacum and its alternative inheritance. Am Nat., **53**: 218–233.

ALKEMINE, M., 1914. Über das Blühen des Reises und einige sich daran anknüpfende Erscheinungen. Zeitschr. für Pflanzenzücht., **2**: 339–375.

ANONYMOUS, 1919. New Iowa oats and the man who found them. Wallace's Farmer, **44**: 771.

ANTHONY, R. D., and HEDRICK, U. P., 1916. Some notes on the breeding of raspberries. New York (Geneva) Agr. Exp. Sta., Bull. 417: 75–88.

ARNY, A. C., and HAYES, H. K., 1918. Experiments in field technic in plot tests. Jour. Agr. Res., **15**: 251–262.

ARNY A. C. and GARBER, R. J., 1918. Variation and correlation in wheat, with special reference to weight of seeds planted. Jour. Agr. Res., **14**: 359–392.

BABCOCK E. B. and CLAUSEN, R. E., 1918. Genetics in relation to agriculture. McGraw-Hill Book Company, New York, 675 pp.

BACKHOUSE, W. O., 1916–17. Note on the inheritance of "crossability." Jour. Genetics, **6**: 91–94.

1918. The inheritance of glume length in T. polonicum. A case of zygotic inhibition. Jour. Genetics, **7**: 125–135.

BAILEY, L. H., 1898. "Evolution of Our Native Fruits." The Macmillan Co., London, 472 pp.

1890. Experiences in crossing cucurbits. Ann. Rept. Cornell Agr. Exp. Sta., **3**: 180–187.

1900. Cyclopedia of American horticulture. The Macmillan Co., New York, I, 410 pp.

1909. Cyclopedia of American agriculture. Vol. 2. Crops. The Macmillan Co., New York, 699 pp.

BAIN, M., and ESSARY, S. H., 1906. Selection for disease-resistant clover. A preliminary report. Tenn. Agr. Exp. Sta., Bull. 75, 10 pp.

BALL, C. R., 1910. The history and distribution of sorghum. U. S. Dept. Agr. Bur. Plant Indust., Bull. 175, 63 pp.

1910. The breeding of grain sorghums. Amer. Breeders' Mag., **1**: 283–293.

1911. The importance and improvement of the grain sorghums. U. S. Dept. Agr., Bur. Plant Indust., Bull. 203, 42 pp.

BALL, C. R. and Piper, C. P., 1916. Contributions to agronomic terminology. Jour. Amer. Soc. Agron., **8**: 1–9, 197–204, 228–237, 310–315.

BALLS, W. L., 1908. Mendelian studies of Egyptian cotton. Jour. of Agr. Sci., **2**: 346–379.

1911 (1913). The inheritance of measurable characters in hybrids between reputed species of cotton. Int. Conf. de Genetique, **4**: 429–440.

1912. The cotton plant in Egypt, studies in physiology and genetics. The Macmillan Co., London, 202 pp.

BARBER, C. W., 1914. Note on the influence of shape and size of plots in tests of varieties of grain. In Maine Agr. Exp. Sta., Bull. 226: 76–84.

BARRUS, M. F., 1918. Varietal susceptibility of beans to strains of Colletotrichum lindemuthianum (Sacc. & Magn.) B. & C. Phytopath., **8**: 589–614.

BATCHELOR, L. D., and REED, H. S., 1918. Relation of the variability of yields of fruit trees to the accuracy of field trials. Jour. Agr. Res., **12**: 245–283.

BAUR, E., 1914. Einführung in die experimentelle Vererbungslehre. Gebrüder Borntræger. Berlin (2nd edition). 401 pp.

BEACH, S. A., 1898. Self-fertility of the grape. New York State Exp. Sta., Bull. 157: 397–441.

1899. Fertilizing self-sterile grapes. New York State Exp. Sta., Bull. 169: 331–371.

1902. Investigations concerning the self-fertility of the grape. New York State Exp. Sta., Bull. 223: 269–290.

BEAL, W. J., 1876–1882. Reports Michigan Board of Agriculture 1876, 1877, 1881 and 1882.

BELLING, J., 1912*a*. Third generation of the cross between velvet and Lyon beans. Rpt. of Florida Agr. Exp. Sta. for 1912: 115–127.

1912*b*. Crossing Corn. Florida Agr. Exp. Sta. Press Bull. 97.

1913. Report of Assistant Botanist. Rpt. of Florida Agr. Exp. Sta. for **1913**: 104–130.

1914*a*. The mode of inheritance of semi-sterility in the offspring of certain hybrid plants. Zeitschr. für Ind. Abstamm. u. Vererb, **12**: 303–342.

1914*b*. Inheritance of pod pubescence and partial sterility in Stizolobium crosses. Rpt. of Florida Agr. Exp. Sta. for **1914**: 31–55.

1915*a*. Inheritance of mottling of the seed-coat. Rpt. of Florida Agr. Exp. Sta. for **1915**: 111–127.

1915*b*. Inheritance of length of pod in certain crosses. Jour. Agr. Res., **5**: 405–420.

BERTHAULT, P., 1911 (1913). Note Preliminaire sur l'origine specifique de la Pomme de Terre. Int. Conf. de Genetique, **4**: 377–380.

BIFFEN, R. H., 1905. Mendel's law of inheritance and wheat breeding. Jour. Agr. Sci., **1**: 4–48.

1907*a*. Studies in the inheritance of disease resistance. Jour. Agr. Sci., **2**: 109–128.

1907*b*. The hybridization of barleys. Jour. Agr. Sci., **2**: 183–206.

1912. Studies in the inheritance of disease resistance. II. Jour. Agr. Sci., **4**: 421–429.

1916. The suppression of characters on crossing. Jour. Genetics, **5**: 225–228.

1917. Systematized plant breeding. In Seward's "Science and the Nation," pp. 146–175. University Press, Cambridge.

BOLLEY, H. L., 1901. Flax wilt and flax sicksoil. North Dakota Agr. Exp. Sta., Bull. 50: 27–57.

1903. Flax and flax seed selection. North Dakota Agr. Exp. Sta., Bull. 55: 171–198.

1909. Some results and observations noted in breeding cereals in a specially prepared disease garden. Proc. Amer. Breeders' Assoc., **5**: 177–182.

BRAND, C. J., 1911. Grimm alfalfa and its utilization in the Northwest. U. S. Dept. Agr., Bur. Plant Indust., Bull. 209, 66 pp.

BURKHOLDER, W. H., 1918. The production of an anthracnose-resistant white marrow bean. Phytopath. **8**: 353–359.

CAPORN, A. ST. CLAIR, 1918. An account of an experiment to determine the heredity of early and late ripening in an oat cross. Jour. Genetics, **7**: 247 – 257.

CARLETON, M. A., 1916. The small grains. The Macmillan Co., New York, 699 pp.

CARRIER, LYMAN, 1919. A reason for the contradictory results in corn experiments. Jour. Amer. Soc. Agron., **11**: 106–113.

COE, H. S., 1918. Origin of the Georgia and Alabama varieties of velvet bean. Jour. Amer. Soc. Agron., **10**: 175–179.

COLLINS, G. N., 1909. The importance of broad breeding in corn. U. S. Dept. Agr., Bur. Plant Indust., Bull. 141: 31–44.

1910*a*. The value of first-generation hybrids in corn. U. S. Dept. Agr., Bur. Plant Indust., Bull. 191, 45 pp.

1910*b*. Increased yields of corn from hybrid seed. Yearbook of U. S. Dept. of Agr. for **1910**: 319–328.

1912. The origin of maize. Jour. Washington Acad. of Sci., **2**: 520–530.

1917. Hybrids of Zea ramosa and Zea tunicata. Jour. Agr. Res., **9**: 383–395.

COLLINS, G. N. and KEMPTON, J. H., 1911. Inheritance of waxy endosperm in hybrids of Chinese maize. Int. Conf. de Genetique, **4**: 347–357.

1913. Effects of cross-pollination on the size of seed in maize. In Misc. Papers, U. S. Dept. Agr., Bur. Plant Indust., Cir. 124.

1914. Inheritance of endosperm texture in sweet × waxy hybrids of maize. Amer. Nat., **48**: 584–594.

COOK, O. F. 1913. Heredity and cotton breeding. U. S. Dept. Agr., Bur. Plant Indust., Bull. 256, 113 pp.

1915. Brachysm, a hereditary deformity of cotton and other plants. Jour. Agr. Res., **3**: 387–400.

CORRENS, C., 1899. Untersuchungen über die Xenien bei Zea Mays. Ber. d. Deutsch. Bot. Ges., **17**: 410–417.

1901. Bastarde zwischen Maisrassen mit besonderer Berücksichtigung der Xenien. Bibliotheca Botanica, **53**: 1–161.

CRANE, M. B., 1915. Heredity of types of inflorescence and fruits in tomato. Jour. Genetics, **5**: 1–11.

CRANDALL, C. S., 1918. Apple-bud selection, apple seedlings from selected trees. Illinois Agr. Exp. Sta., Bull. 211: 181–264.

Cummings, M. B., 1904. Fertilization problems: A study of reciprocal crosses. Maine Agr. Exp. Sta. Bull., 104: 81–99.

Cutler, G. H., 1919. A dwarf wheat. Jour. Amer. Soc. Agron., **11**: 76–78.

Darwin, Charles, 1877. The effects of cross- and self-fertilization in the vegetable kingdom. Appleton & Co., London.

De Candolle, Alphonse, 1886. Origin of cultivated plants. Kegan Paul, Trench & Co., London, 468 pp.

Dettweiler, 1914. Aryan agriculture. Jour. Heredity, **5**: 473–481.

De Vries, Hugo, 1899. Sur la fecondation hybride de l'albumen. Comptes Rend. des Seances de l'Academe des Seances, **129**: 973–975.

1906. Species and varieties: their origin by mutation. Open Court Pub. Co., Chicago.

1907. Plant breeding. Open Court Pub. Co., Chicago, 360 pp.

Dillman, A. C., 1916. Breeding millet and sorgo for drought adaptation. U. S. Dept. of Agr., Bull. 291, 19 pp.

Don, George, 1838. A general history of the dichlamydeous plant. Vol. IV. Corollifloræ.

Dorsey, M. J., 1914. Pollen development in the grape with special reference to sterility. Minnesota Agr. Exp. Sta., Bull. 144: 3–60.

1916. The inheritance and permanence of clonal varieties. Proc. Amer. Soc. Hort. Sci., for **1916**: 1–31.

1919. A study of sterility in the plum. Genetics, **4**: 417–488.

Durst, C. E., 1918. Tomato selection for fusarium resistance. Phytopath., **8**: 80.

East, E. M., 1907. The relation of certain biological principles to plant breeding. Connecticut Agr. Exp. Sta., Bull. 158, 92 pp.

1908*a*. Some essential points in potato breeding. Conn. Agr. Exp. Sta. Ann. Report for **1907–08**: 429–447.

1908*b*. A study of the factors influencing the improvement of the potato. Illinois Agr. Exp. Sta., Bull. 127: 375–456.

1908*c*. Inbreeding in corn. Conn. Agr. Exp. Sta. Rept. for **1907**: 419–428.

1910*a*. The transmission of variations in the potato in asexual reproduction. Conn. Agr. Exp. Sta. Rept. for **1909–10**: 119–160.

1910*b*. Inheritance in potatoes. Am. Nat., **44**: 424–430.

1910*c*. The rôle of hybridization in plant breeding. Popular Science Monthly, Oct., **1910**: 342–355.

1910*d*. Note on an experiment concerning the nature of unit characters. Science. N. S. **32**: 93–95.

1912*a*. A study of hybrids between Nicotiana bigelovii and N. quadrivalvis. Bot. Gaz., **53**: 243–248.

1912*b*. Inheritance of color in the aleurone cells of maize. Am. Nat., **46**: 363–365.

1916*a*. Studies on size inheritance in Nicotiana. Genetics, **1**: 164–176.

1916*b*. Inheritance in crosses between Nicotiana langsdorffii and Nicotiana alata. Genetics, **1**: 311–333.

1919*a*. Studies on self-sterility III. The relation between self-fertile and self-sterile plants. Genetics, **4**: 340–345.

1919*b*. Studies on self-sterility IV. Selective fertilization. Genetics, **4**: 346–355.

1919*c*. Studies on self-sterility V. A family of self-sterile plants wholly cross-sterile inter se. Genetics, **4**: 356–363.

East, E. M. and Hayes, H. K., 1911. Inheritance in maize. Conn. Agr. Exp. Sta., Bull. **167**: 142 pp.

1912. Heterozygosis in evolution and in plant breeding. U. S. Dept. Agr., Bur. Plant Indust., Bull. 243, 58 pp.

East, E. M. and Jones, D. F., 1919. Inbreeding and outbreeding. J. B. Lippincott Co., Philadelphia, 285 pp.

East, E. M. and Park, J. B., 1917. Studies on self-sterility I. The behavior of self-sterile plants. Genetics, **2**: 505–609.

1918. Studies on self-sterility II. Pollen tube growth. Genetics, **3**: 353–366.

Edgerton, C. W., 1918. A study of wilt-resistance in the seed-bed. Phytopath., **8**: 5–14.

Emerson, R. A., 1910. The inheritance of sizes and shapes in plants. Am. Nat., **44**: 739–746.

1911. Genetic correlation and spurious allelomorphism in maize. Ann. Rept. Nebraska Agr. Exp. Sta., **24**: 59–90.

1912*a*. The unexpected occurrence of aleurone colors in F_2 of a cross between non-colored varieties of maize. Am. Nat., **46**: 612–615.

1912*b*. The inheritance of the ligule and auricles of corn leaves. Ann. Rpt. of Nebraska Exp. Sta., **25**: 81–88.

1914*a*. The inheritance of recurring somatic variation in variegated ears of maize. Neb. Agr. Exp. Sta. Res., Bull. 4: 35 pp.

1914*b*. Multiple factors vs. "Golden Mean" in size inheritance. In Science, N. S., **40**: 57–58.

1916. A genetic study of plant height in Phaseolus vulgaris. Neb. Agr. Exp. Sta. Res., Bull. **7**: 73 pp.

1917. Genetical studies of variegated pericarp in maize. Genetics, **2**: 1–35.

1918. A fifth pair of factors, Aa, for aleurone color in maize, and its relation to the Cc and Rr pairs. N. Y. Cornell Univ. Exp. Sta. Memoir, **16**: 231–289.

Emerson, R. A. and East, E. M., 1913. The inheritance of certain quantitative characters in maize. Neb. Agr. Exp. Sta. Res., Bull. 3: 120 pp.

Engledow, F. L., 1914. A case of repulsion in wheat. Proc. Cambridge Phil. Soc., **17**: 433–435.

Etheridge, W. C., 1916. A classification of the varieties of cultivated oats. New York Cornell Univ. Exp. Sta., Memoir, **10**: 167 pp.

Farrer, W., 1898. The making and improving of wheats for Australian conditions. Agr. Gaz. of N. S., Wales, **10**: 131–168.

Fletcher, S. W., 1911. Pollination of the Bartlett and Kieffer pears. Virginia Agr. Exp. Sta. Rept. for **1909–10**: 213–224.

1916. North American varieties of the strawberry. Virginia Agr. Exp. Sta., Tech. Bull. **11**: 3–126.

Focke, W. O., 1881. Die Pflanzen-mischlinge. Borntræger, Berlin, 569 pp.

FRANDSEN, H. N., 1917. Die Befruchtungsverhältnisse bei Grass und Klee in ihrer Beziehung zur Züchtung. Zeitschr. für Pflanzenzucht., **5**.

FRASER, A. C., 1919. The inheritance of the weak awn in certain Avena crosses and its relation to other characters of the oat grain. Cornell Univ. Agr. Exp. Sta. Memoir, **23**: 635–676.

FREAR, D. W., 1915. Crossing of wheat flowers unprotected after emasculation. Jour. Heredity, **6**: 350.

FREEMAN, G. F., 1917. Linked quantitative characters in wheat crosses. Am. Nat., **51**: 683–689.

1918. Producing breadmaking wheats for warm climates. Jour. Heredity, **9**: 211–226.

1919. Heredity of quantitative characters in wheat. Genetics, **4**: 1–93.

FRUWIRTH, CARL, 1909. Die Züchtung der landwirtschaftlichen Kulturpflanzen. Paul Parey, Berlin. Bd. II, 2 Auflage., Maize, pp. 5–40. Bd. III, 2 Auflage., Flax, pp. 47–60. Bd. IV, 2 Auflage., Wheat, pp. 107–186; Barley, pp. 240–321; Oats, pp. 324–365; Rye, pp. 187–239; Bd. V, 2 Auflage., Rice, pp. 36–54.

1912. Zur Züchtung der Kartoffel, Deut. Landw, Presse. **39**: 551–552, 565–567.

1917. Selection in pure lines. Jour. Heredity, **8**: 90–94.

GAINES, E. F., 1917. Inheritance in wheat, barley and oat hybrids. Washington Agr. Exp. Sta., Bull. 135: 3–61.

1918. Comparative smut resistance of Washington wheats. Jour. Amer. Soc. Agron., **10**: 218–222.

1920. The inheritance of resistance to bunt or stinking smut of wheat. Jour. Amer. Soc. Agron., **12**: 124–132.

GALLOWAY, B. T., 1907. Progress in some of the new work of the Bureau of Plant Industry. Yearbook of U. S. Dept. of Agr. for **1907**: 139–141.

GARBER, R. J., 1921. A Preliminary Note on the Inheritance of Rust Resistance in Oats. Jour. Amer. Soc. Agron., **13**: 41–43.

GARBER, R. J., and OLSON, P. J., 1919. A study of the relation of some morphological characters to lodging in cereals. Jour. Am. Soc. Agron., **11**: 173–186.

GARNER, W. W., 1912. Some observations on tobacco breeding. Am. Breeders' Assoc. Rept., **8**: 458–468.

GARNER, W. W., and ALLARD, H. A., 1920. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. Jour. Agric. Research, **18**: 553–606.

GÄRTNER, G. F., 1849. Versuche und Beobachtungen uber die Bastarderzeugung im Pflanzenreich. Stuttgart, Hering & Comp., 791 pp.

GATES, R. R., 1911. Mutation in Oenothera. Am. Nat., **45**: 577–606.

GILBERT, A. W., 1917. The potato. The Macmillan Co., New York, 318 pp.

GOFF, E. S., 1894. Flowering and fertilization of the native plum. Gard. and For., **7**: 262–263.

1901. Native plums. Wis. Agr. Exp. Sta., Bull. 87, 31 pp.

GOODSPEED, T. H., 1912. Quantitative studies of inheritance in Nicotiana hybrids. I. Univ. Calif. Pub. on Botany **5**: 87–168.

1913. Quantitative studies of inheritance in Nicotiana hybrids. II. Univ. Calif. Pub. on Botany, **5**: 169–188.

1915. Parthenocarpy and parthenogenesis in Nicotiana. Proc. Nat. Acad. Sci., **1**: 341–346.

GOODSPEED, T. H. and CLAUSEN, R. E., 1917. Mendelian factor differences versus reaction system contrasts in heredity. Am. Nat., **51**: 31–46, 92-101.

GRAHAM, R. J. D., 1916. Pollination and cross-fertilization in the Juar plant (Andropogon Sorghum, Brot.). Mem. Dept. Agr. India Bot. Ser., **8**: 201–216.

GROTH, B. H. A., 1910. Structure of tomato skins. New Jersey Agr. Exp. Sta., Bull. 228, 20 pp.

1911. The F_1 heredity of size, shape, and number in tomato leaves. Parts 1 and 2. New Jersey Agr. Exp. Sta., Bull. 238 and 239.

1912. The F_1 heredity of size, shape, and number in tomato fruits. New Jersey Agr. Exp. Sta., Bull. 242.

1914. The "Golden Mean" in the inheritance of size. In Science, N. S., **39**: 581–584.

1915. Some results in size inheritance. New Jersey Agr. Exp. Sta., Bull. 278.

GUIGNARD, M. L., 1899. Sur les anthérozoides et la double copulation sexuelle chez les vegetaux angiospermes. Rev. génér. d. Bot., **11**: 129–135.

1901. La double fecondation dans le mais. Jour. de Bot., **15**: 37–50.

HAGEDOORN, A. L., and A. C., 1914. Studies on variation and selection. Zeitschr. für Induk. Abst. u. Vererb., **11**: 145–183.

HANSEN, N. E., 1911. Some new fruits. South Dakota Agr. Exp. Sta., Bull. 130: 163–200.

1915. Progress in plant breeding. South Dakota Agr. Exp. Sta., Bull. 159: 179–192.

HARLAN, H. V., 1918. The identification of varieties of barley. U. S. Dept. Agr., Bur. Plant Indust., Bull. 622, 32 pp.

1920 Smooth Awned barleys, Jour. Amer. Soc. Agron. **12**: 205-208.

HARLAN, H. V., and ANTHONY, S. B., 1920. Development of barley kernels in normal and clipped spikes and the limitations of awnless and hooded varieties. Jour. Agric. Res., **19**: 431–472.

HARLAN, H. V. and HAYES, H. K., 1920. The occurrence of the fixed intermedium Hordeum intermedium haxtoni in crosses between H. vulgare pallidum and H. distichon. Jour. Agr. Res., **19**: 575–591.

HARLAND, S. C., 1917. On the inheritance of the number of teeth in the bracts of Gossypium. West Indian Bull., **16**: 111–120.

1919*a*. Notes on inheritance in the cowpea. Agr. News. Barbados, **18**: 20.

1919*b*. Notes on inheritance in the cowpea. Agr. News. Barbadose **18**: 68.

1919*c*. Inheritance of certain characters in the cowpea (Vigna sinnesis). Jour. Genetics, **8**: 101–132.

1920. Inheritance of certain characters in the cowpea. (Vigna sinnsis.), II. Jour. Genetics, **10**: 193–205.

HARRIS, J. A., 1915. On a criterion of substratum homogeneity (or heterogeneity) in field experiments. Am. Nat., **49**: 430–454.

HARSHBERGER, J. W., 1897. Maize: A botanical and economic study. In Contritubions from the Botanical Laboratory, Univ. of Pennsylvania, **1**: 75–202.

1904. A study of the fertile hybrids produced by crossing teosinte and maize. In Contributions from the Botanical Laboratory, Univ. of Pennsylvania, **2**: 231–235.

1909. Maize, or Indian corn. Cyclopedia of American agriculture, **2**: 398–402.

HARTLEY, C. P.; BROWN, ERNEST B.; KYLE, C. H.; and ZOOK, L. L., 1912. Crossbreeding corn. U.S. Dept. Agr., Bur. Plant Indust., Bull. 218: 5–72.

HASSELBRING, H., 1912. Types of Cuban tobacco. Bot. Gaz., **53**: 113–126.

HAYES, H. K., 1912. Correlation and inheritance in Nicotiana tabacum. Conn. Agr. Exp. Sta., Bull. 171, 45 pp.

1913*a*. Corn improvement in Connecticut. Conn. Agr. Exp. Sta. Rept. for **1913**: Part VI, 353–384.

1913*b*. The inheritance of certain quantitative characters in tobacco. Zeitschr. für Induk. Abstamm. u. Vererb., **10**: 115–129

1914. Variation in tobacco. Jour. Heredity, **5**: 40–46.

1915. Tobacco mutations. Jour. Heredity, **6**: 73–78.

1917. Inheritance of a mosaic pericarp pattern color of maize. Genetics, **2**: 261–281.

1918*a*. Natural cross-pollination in wheat. Jour. Am. Soc. Agron., **10**: 120–122.

1918*b*. Normal self-fertilization in corn. Jour. Am. Soc. Agron., **10**: 123–126

1918*c*. Natural crossing in wheat. Jour. Heredity, **9**: 326–330.

HAYES, H. K. and ARNY, A. C., 1917. Experiments in field technic in rod-row tests. Jour. Agr. Res., **11**: 399–419.

HAYES, H. K. and BEINHART, E. G., 1914. Mutation in tobacco. Science N. S. **39**: 34–35.

HAYES, H. K. EAST, E. M. and BEINHART, E. G., 1913. Tobacco breeding in Connecticut. Conn. Agr. Exp. Sta., Bull. 176.

HAYES, H. K. and EAST, E. M., 1911. Improvement in corn. Conn. Agr. Exp. Sta., Bull. 168: 3–21.

1915. Further experiments on inheritance in maize. Conn. Agr. Exp. Sta., Bull. 188, 31 pp.

HAYES, H. K. and GARBER, R. J., 1919. Breeding small grains in Minnesota. Part 1. Technic and results with wheat and oats. Minnesota Agr. Exp. Sta., Bull. 182.

1919. Synthetic production of high-protein in corn in relation to breeding. Jour. Am. Soc. Agron., **11**: 309–318.

HAYES, H. K. and HARLAN, H. V., 1920. The inheritance of the length of internode in the rachis of the barley spike. U. S. Dept. Agr. Bull. 869, 26 pp.

HAYES, H. K. and JONES, D. F., 1916. The effects of cross- and self-fertilization in tomatoes. Conn. Agr. Exp. Sta. Ann. Rept. for **1916**: 305–318.

HAYES, H. K. and JONES, D. F., 1916. First generation crosses in cucumbers. Conn. Agr. Exp. Sta. Ann. Rept. for **1916**: 319–322.

HAYES, H. K. and OLSON, P. J., 1919. First generation crosses between standard Minnesota corn varieties. Minnesota Agr. Exp. Sta., Bull. 183: 4–22.

HAYES, H. K. PARKER, J. H., and KURTZWEIL, CARL, 1920. Genetics of rust resistance in crosses of varieties of Triticum vulgare with varieties of T. durum and T. dicoccum. Jour. Agr. Res., **11**: 523–542.

HAYES, H. K. and STAKMAN, E. C., 1919. Rust resistance in timothy. Jour. Am. Soc. Agron., **11**: 67–70.

HAYS, W. M., and BOSS, ANDREW, 1899. Wheat. Varieties, breeding, cultivation. Minnesota Agr. Exp. Sta., Bull. 62: 321–494.

HAYS, W. M., 1901. Plant breeding. U. S. Dept. Agr., Div. Veg. Phys. and Path. Bull. 29, 72 pp.

HECKEL, E., 1909. Fixation de la mutation germinaire culturale du Solanum maglia: variation de forme et de coloris des tubercules unites. Compt. Rend. l' Acad. Sci., **149**: 831–833.

1912. Sur la mutation germinaire culturale du Solanum tuberosum L. Compt. Rend. l' Acad. Sci., **155**: 469–471.

HECTOR, G. P., 1913. Notes on pollination and cross-fertilization in the common rice plant, Oryza sativa, Linn. Mem. Dept. Agr. India, Bot. Ser., 6: 1–10.

1916. Observation on the inheritance of anthocyan pigment in paddy varieties. Mem. Dept. Agr. India, Bot. Ser., **8**: 89–101.

HEDRICK, U. P., and BOOTH, N. O., 1907. Mendelian characters in tomatoes. Proc. Soc. for Hort. Sci., **5**: 19–24.

HEDRICK, U. P. and ANTHONY, R. D., 1915. Inheritance of certain characters of grapes. N. Y. (Geneva) Agr. Exp. Sta., Tech. Bull. 45: 3– 9.

HEDRICK, U. P. and WELLINGTON, R., 1912. An experiment in breeding apples. N. Y. (Geneva) Agr. Exp. Sta., Bull. 350: 141–186.

HENKEMEYER, A., 1915. Untersuchungen über die Spaltungen von Weizenbastarden in der F_2 und F_3 Generation. Jour. für Land., **63**: 97–124.

HILSON, G. R., 1916. A note on the inheritance of certain stem characters in sorghum. Agr. Jour. of India, **11**: 150–155.

HOPKINS, C. G., 1899. Improvement in the chemical composition of the corn kernel. Illinois Agr. Exp. Sta., Bull. 55: 205–240.

HOSHINO, Y., 1915. On the inheritance of the flowering time in peas and rice. Jour. Col. Agr. Tokoku U. (Sapporo), **6**: 229–288.

HOUSER, TRUE, 1912. Certain results in Ohio tobacco breeding. Am. Breeders' Assoc. Rept., **8**: 468–479.

HOWARD, A.; HOWARD, G.; and RAHMAN KAHN, ABDUL, 1910*a*. The economic significance of natural cross-fertilization in India. Mem. Dept. Agr. India, Bot. Ser., **3**:

1919. Studies of the pollination of crops. I. Mem. Dept. Agr. India, Bot. Ser., **10**: 195–220.

HOWARD, A; and HOWARD, G. L. C., 1910*b*. Studies in Indian tobaccos, No. 1. The types of Nicotiana rustica L. Yellow-flowered tobacco. Mem. Dept. Agr. India, Bot. Ser., **3**: 1–58.

1910*c*. Studies in Indian tobaccos, No. 2. The types of Nicotiana tabacum L. Mem. Dept. Agr. India, Bot. Ser., **3**: 59–176.

1912. On the inheritance of some characters in wheat. Mem. Dept. Agr. India, Bot. Ser., **5**: 1–47.

1915. On the inheritance of some characters in wheat. II. Mem. Dept. Agr. India, Bot. Ser., **7**: 273–285.

HOWARD, G. L. C., 1913. Studies in Indian tobaccos, No. 3. The inheritance of characters in Nicotiana tabacum L. Mem. Dept. Agr. India, Bot. Ser., **6**: 25–114.

HUTCHESON, T. B., 1914. Thirteen years of wheat selection. Am. Nat., **48**: 459–466.

HUTCHESON, T. B. and WOLFE, T. K., 1917. The effect of hybridization on maturity and yield in corn. Virginia Agr. Exp. Sta., Tech. Bull. 18: 161–170.

IKENO, S., 1913. Studien über die Bastarde von Paprika (Capsicum annuum). Zeitschr. für Induk. Abstamm. u. Vererb., **10**: 99–114.

1914. Über die Bestaubung und die Bastardierung von Reis. Zeitschr. für Pflanzenzücht., **2**: 495–503.

1918. "Zikken-Idengaku" (a text-book on genetics) (Japanese). 3rd edition. Nippon-no Romazi-Sya, Tokyo. Abstract in Bot. Abstracts, **2**: 114, 115.

JARDINE, W. M., 1917. A new wheat for Kansas. Jour. Am. Soc. Agron., **9**: 257–266.

JELINEK, J., 1918. Beitrag zur Technik der Weizenbastardierung. Zeitschr. für Pflanzenzücht., **6**: 55–57

JENKINS, E. H., 1914. Studies on the tobacco crop of Connecticut. Conn. Agr. Exp. Sta., Bull. 180, 65 pp.

JENSEN, H., 1907. Tobacco experiments. Jaarb. Dept. Landb. Nederland. Indie, **1907**: 199–217. Abstract in Exp. Sta. Record, **20**: 935.

JESENKO, F., 1911 (1913). Sur un hybride fertile entre Triticum sativum ♀ (Ble Mold Squarehead) et Secale cereale ♂ (Seigle de Petkus). Int. Conf. de Genetique, **4**: 501–511.

1913. Über Getreide—Speziesbastarde (Weizen-Roggen). Zeitschr. für Induk. Abstamm. u. Vererb., **10**: 311–326.

JOHANNSEN, W., 1903. Ueber Erblichkeit in Populationen und in reinen Linien. G. Fischer, Jena., 68 pp.

1909. Elemente der exakten Erblichkeitslehre. G. Fischer, Jena., 723 pp.

JOHNSON, D. S., 1915. Sexuality in plants. Jour. Heredity, **6**: 3–16.

JOHNSON, J., 1919. An improved strain of Wisconsin tobacco. Jour. Heredity, **10**: 281–288.

1919. Inheritance of branching habit in tobacco. Genetics, **4**: 307–340.

JONES, D. F., 1916. Natural cross pollination in the tomato. Science N. S., **43**: 509–510.

1917. Linkage in Lycopersicum. Am. Nat., **51**: 608–621.

1918. The effects of inbreeding and cross-breeding upon development. Conn. Agr. Exp. Sta., Bull. 207, 100 pp.

1919. Selection of pseudo-starchy endosperm in maize. Genetics, **4**: 364–393.

1920. Selection in self-fertilized lines as a basis for corn improvement, Jour. Amer. Soc. Agron., **12**: 77–100.

JONES, D. F., 1920. Heritable characters of maize—Defective seeds. Jour. Heredity, **11**: 161–167.

JONES, D. F. and GALLASTEGUI, G. A., 1919. Some factor relations in maize with reference to linkage. Am. Nat., **53**: 239–246.

JONES, D. F., HAYES, H. K., SLATE, JR., W. L., and SOUTHWICK, B. G., 1917. Increasing the yield of corn by crossing. Conn. Agr. Exp. Sta. Rept. for **1916**: 327–347.

JONES, L. R., and GILMAN, J. C., 1915. The control of cabbage yellows through disease resistance. Wis. Agr. Exp. Sta., Res. Bull. 38, 70 pp.

JONES, L. R., WALKER, J. C., and TISDALE, W. B., 1920. Fusarium Resistant Cabbage. Wisconsin Agr. Exp. Sta., Res. Bull. 48: 3–34.

KAJANUS, B., 1913. Über die Vererbungsweise gewisser Merkmale der Beta- und Brassica-Rüben. Zeitschr. für Pflanzenzücht., **1**: 125—186.

KARPER, R. E., and CONNER, A. B., 1919. Natural cross-pollination in milo. Jour. Am. Soc. Agron., **11**: 257–259.

KEARNEY, T. H., 1914. Mutation in Egyptian cotton. Jour. Agr. Res., **2**: 287–302.

KEEBLE, F., and PELLEW, C., 1910. The mode of inheritance of stature and of time of flowering in peas (Pisum sativum). Jour. Genetics, **1**: 47–56.

KEZER, ALVIN and BOYACK, BREEZE, 1918. Mendelian inheritance in wheat and barley crosses. Colorado Agr. Exp. Sta., Bull. 249, 139 pp.

KIESSELBACH, T. A., 1916. Recent developments in our knowledge concerning corn. Nebraska Corn Improv. Assoc. Rept., **7**: 15–42.

1918. Studies concerning the elimination of experimental error in comparative crop tests. Nebraska Agr. Exp. Sta., Res. Bull. 13, 95 pp.

KIESSELBACH, T. A. and RATCLIFF, J. A., 1917. Oats investigations. Nebraska Agr. Exp. Sta., Bull. 160. 48 pp.

KIRCHNER, O., 1886. Flora von Stuttgart und Umgebung, mit besonderer Berücksichtigung der Pflanzenbiologischen Verhältnisse., Stuttgart.

KNIGHT, L. I., 1917. Physiological aspects of self-sterility of the apple. Proc. Am. Soc. Hort. Sci., **1917**: 101–105.

KNIGHT, T. A., 1841. Philisophical transactions. See "Knight's Collected Works," London (1799).

KNUTH, PAUL, 1909. Handbook of flower pollination. Translation by Davis. Clarendon Press. Vol. II, Flax, p. 216. Vol. III, Maize, p. 518, wheat, p. 529, oats, p. 524, barley, p. 532, rye, p. 531, rice, p. 521.

KOCK, L., 1917. Experiments on the artificial hybridization of rice in Java. Int. Rev. Sci. and Prac. Agr., **8**: 1240–1241.

KÖLREUTER, J. G., 1766. Dritte Fortsetzung der vorläufigen Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen. Gleditschen Handlung. Reprinted 1893 in Ostwald's Klassiker der exakten Wissenschaften No. 41. Leipzig: Engelmann.

KUWADA, Y., 1919. Die Chromosomenzahl von Zea mays, L. Ein Beitrag zur Hypothesa der Individualität der Chromosomen und zur Frage über die Herkunft von Zea mays, L. Jour. Coll. Sci. Imperial Univ. Tokyo, **39**: 1–148. Abst. by Ikeno, S. in Bot. Absts., **4**: 104, 1920.

LEAKE H. M., 1911. Studies in Indian cotton. Jour. Genetics, **1**: 205–272.

LEIDIGH, A. H., 1911. Methods for the improvement of sorghum. Am. Breeders' Mag., **2**: 294–295.

LEIGHTY, C. E., 1915. Natural wheat-rye hybrids. Jour. Am. Soc. Agron., **7**: 209–216.

1916. Carman's wheat-rye hybrids. Jour. Heredity, **7**: 420–427.

LEIGHTY, C. E., and HUTCHESON, T. B., 1919. On the blooming and fertilization of wheat flowers. Jour. Am. Soc. Agron., **11**: 143–162.

LINDSTROM, E. W., 1918. Chlorophyll inheritance in maize. New York Cornell Agr. Exp. Sta., Mem. 13: 3–68.

LEWIS, C. I., and VINCENT, C. C., 1909. Pollination of the apple. Oregon Agr. Exp. Sta., Bull. 104, 3–40.

LOTSY, J. P., 1916. Evolution by means of hybridization. The Hague, Martinus Nykoff, pp. 68–75.

LOVE, H. H., 1914. Oats for New York. N. Y. Cornell Agr. Exp. Sta., Bull. 343: 362–416.

LOVE, H. H. and CRAIG, W. T. 1918*a*. Methods used and results obtained in cereal investigations at the Cornell station. Jour. Am. Soc. Agron., **10**: 145–157.

1918*b*. Small grain investigations. Jour. Heredity, **9**: 67–76.

1918*c*. The relation between color and other characters in certain Avena crosses. Am. Nat., **52**: 369–383.

1919*a*. Fertile wheat-rye hybrids Jour. Heredity, **10**: 195–207.

1919*b*. The synthetic production of wild wheat forms. Jour. Heredity, **10**: 51–64.

LOVE, H. H. and MCROSTIE, G. P. 1919. The inheritance of hull-lessness in oat hybrids. Am. Nat., **53**: 5–32.

LUMSDEN, D., 1914. Mendelism in melons. New Hampshire Agr. Exp. Sta., Bull. 172; 58 pp.

MCCLELLAND, C. K., 1919. The velvet bean. Georgia Agr. Exp. Sta., Bull. 129: 83–98.

MCFADDEN, E. A., 1917. Wheat-rye hybrids. Jour. Heredity, **8**: 335–336.

MCLENDON, C. A., 1912. Mendelian inheritance in cotton hybrids. Georgia Agr. Exp. Sta., Bull. 99: 139–228.

MCROSTIE, G. P., 1919. Inheritance of anthracnose resistance as indicated by a cross between a resistant and a susceptible bean. Phytopath., **9**: 141–148.

1921. Inheritance of Disease Resistance in the Common Bean. Jour. Amer. Soc. Agron., **13**: 15–32.

MACDOUGAL, D. T., 1916. Analysis of a potato hybrid, Solanum fendleri × S. tuberosum. Carnegie Inst. Yearbook, **16**: 98.

MACOUN, W. T. 1915. Plant breeding in Canada. Jour. Heredity, **6**: 398–403.

1918. The potato in Canada. Canadian Exp. Farm, Bull. 90: 3–100.

MALTE, M. O. and MACOUN, W. T., 1915. Growing field root, vegetable and flower seeds in Canada. Canadian Dept. of Agr., Bull. 22, Second series, 15 pp.

MARTIN, J. N., 1913. The physiology of the pollen of Trifolium pratense. Bot. Gaz., **56**: 112–126.

MAYER-GMELIN, H., 1917. De Kruising van roode onge baarde spelt met fluweelkaf Essex-Tarwe een voorbeeld van Factoren-analyze. Cultura **29**: 141–159. See Abstract Bulletin Monthly Intelligence and Plant Diseases, **8**: 1236–1239 (1917), Zeitschr. für Induk. Abstamm. u. Vererb., **29**: 51 (1918).

MENDEL, GREGOR JOHANN, 1909. Experiments in plant hybridization. In Bateson's "Mendel's Principles of Heredity," pp. 317–368. 1909. Translated by Royal Horticultural Society.

MERCER, W. B., and HALL, A. D., 1911. The experimental error of field trials. Jour. Agr. Sci., **4**: 107–132.

MILLER, EDWIN C., 1919. Development of the pistillate spikelet and fertilization in Zea Mays L. Jour. Agr. Res., **18**: 255–265.

MIYAZAWA, B., 1918. Oomugi no mi no iro iden ni tuite (on the inheritance of the fruit-color of barley). Bot. Mag. Tokyo, **32**: 308–310. Abstract in Bot. Abstrs., **1**: 243 Entry. 1537: 1919.

MONTGOMERY, E. G., 1906. What is an ear of corn? Popular Sci. Mthly., **68**: 55–62.

1909. Experiments with corn. Nebraska Agr. Exp. Sta., Bull. 112: 5–36.

1912. Wheat breeding experiments. Nebraska Agr. Exp. Sta., Bull. 125, 16 pp.

1913. Experiments in wheat breeding. U. S. Dept. Agr., Bur. Plant Indust., Bull. 269, 61 pp.

MORROW, G. E., and GARDNER, F. D., 1893. Field experiments with corn. Illinois Agr. Exp. Sta., Bull. 25: 173–203.

1894. Experiments with corn. Illinois Agr. Exp. Sta., Bull. 31: 359–360.

MUNSON, W. M., 1906. Plant breeding in relation to American pomology. Maine Agr. Exp. Sta., Bull. 132: 149–176.

NABOURS, ROBERT K., 1919. Parthenogenesis and crossing-over in the grouse locust Apotettix. Am. Nat. **53**: 131–142.

NAUDIN, CH., 1856. Nouvelles recherches sur les caracters specifiques et les varietes des plantes du genre Cucubita. Ann. d. Sci. Nat. Fourth series, **6**: 5–73.

1859*a*. Especes et des varietes du genre Cucumis. Ann. d. Sci. Nat. Fourth series, **11**: 1–87.

1859*b* Revue des Cucurbitacees. Ann. d. Sci. Nat. Fourth series, **12**: 79–164.

1865. Nouvelles recherches sur' l'hybridite dans les vegetaux. Nouvelles archives du' Museum d' Histoire Naturelle de Paris I. 25–176.

NAWASCHIN, S., 1898. Resultate einer Revision der Befruchtungsvorgänge bei Lilium martagon und Fritillaria tenella. Bull. Acad. Imp. Sci. St. Petersbourg. s. 5, t. 9, No. 4: 377–382.

NEALE, S. T., 1901. Pedigreed sorghum as a source of cane sugar. Delaware Agr. Exp. Sta., Bull. 51, 24 pp.

NEWMAN, L. H., 1912. Plant breeding in Scandinavia. Ottawa, Canada, 193 pp.

NILSSON-EHLE, H., 1908. Einige Ergebnisse von Kreuzungen bei Hafer und Weizen. Botan. Notiser, Lund., pp. 257–298.

1909. Kreuzungsuntersuchungen an Hafer und Weisen. Lunds. Univ. Arsskr. N. F. Afd. 2, Bd. 5 Rr. 2pp. 122.

1911*a*. Ueber Fälle spontanen Wegfallens eines Hemmungsfaktors beim Hafer Zeitzchr. für Induk. Abstamm. u. Vererb., 5: 1–37.

1911*b*. Kreuzungsuntersuchungen an Hafer und Weizen. Lunds. Univ. Arsskr. N. F. Afd.2, Bd. 7, Nr. 6, pp. 3–84.

1911*c*. Mendelisme et Acclimatation. Int. Conf. de Genetique, **4**: 1–22.

1912. Zur Kenntnis der Erblichskeitsverhältnisse der Eigenschaft Winterfestigkeit beim Weizen. Zeitschr. für Pflanzenzucht., **1**: 3–12.

1915. Gibt es erbliche Weizenrassen mit mehr oder weniger vollständiger Selbstfruchtung? Zeitschr. für Pflanzenzücht., **3**: 1–6.

1917. Improvement of black oats by selection and crossing in Sweden. Int. Rev. Sci. and Prac. of Agr. Year 8, No. 5: 712–715.

NILSSON, H. N., 1901. Forteckning öfver de vigtigarte sorteng pa Sveriges utsädes forenings försöksfält. Sveriges Utsäd. Tidskr., 1901, 66–104. From Etheridge, 1916.

1912–13. Potatis foradling och potatis bedömning. Weibulls arsbok, **8**: 4–31. 1913. Abstract by author in Zeitschr. für Pflanzenzücht., **1**: 240–242, 1912–1913.

NILSSON, HERIBERT, 1916. Populations analysen und Erblichkeitsversuche über die Selbststerelität, Selbstfertilität, und Sterilität bei dem Roggen. Zeitschr. für Pflanzenzücht., **4**: 1–44

NOHARA, S., 1918. Endô no keisitu iden ni tuite. (On the inheritance of certain characters in the pea). (In Japanese) Nippon Ikusyugakukwai Kwaiho (Rep. Jap. Assoc. Breeding Sci.) **22**: 12–14, 1918. Genetic studies in some characters in Pisum Bot. Mag. Tokyo **32**: 91–102, 1918. Abstract by S. Ikeno in Bot. Abstrs., **1**: 87. Entry 491, 1918.

NORTON, J. B., 1902. Improvement of oats by breeding. Proc. Int. Conf. Plant Breeding and Hybridization, **1**: 103–109.

1907. Notes on breeding oats. Proc. Am. Breeders, Assoc., **3**:280–285.

1911–12. Asparagus breeding. Am. Breeders' Assoc. Rept., **7 & 8**: 440–444.

1913. Methods used in breeding asparagus for rust resistance. U. S. Dept. Agr., Bur. Plant Indust., Bull. 263, 60 pp.

1919. Washington asparagus: Information and suggestions for growers of new pedigreed rust-resistant strains. U. S. Dept. Agr., Bur. Plant Indust., Cotton, Truck and Forage Crop Disease Invest. Cir. **7**: 2–8.

OLIVER, G. W., 1910. New Methods of plant breeding. U. S. Dept. Agr., Bur. Plant Indust., Bull. 167, 39 pp.

OLSON, P. J.; BULL, C. P.; and HAYES, H. K., 1918. Ear type selection and yield in corn. Minnesota Agr. Exp. Sta., Bull. 174: 3–60.

ORTON, W. A., 1902. The wilt disease of the cowpea and its control. Part I. U. S. Dept. Agr., Bur. Plant Indust., Bull. 17: 9–22.

1911 (1913). The development of disease resistant varieties of plants. Int. Conf. de Genetique, **4**: 247–261.

1914. Potato wilt, leaf roll, and related diseases. U. S. Dept. Agr., Bull. 64, 48 pp.

PAMMEL, L H., 1892. On the crossing of cucurbits. Iowa Agr. Exp. Sta., Bull. 19: 595–600.

PARKER, JOHN H., 1918. Greenhouse experiments on the rust resistance of oat varieties. U. S. Dept. Agr., Bull. 629, 1–16.

1920. A preliminary study of the inheritance of rust resistance in oats. Jour. Am. Soc. Agron., **12**: 23–38.

PARKER, W. H., 1914. Lax and dense-eared wheats. Jour. Agr. Sci., **6**: 371–386.

PARNELL, F. R., AYYANGAR, G. N. R., and RAMIAH, K., 1917. The inheritance of characters in rice. I. Mem. Dept. Agr. India, Bot. Ser., **9**: 75–105.

PEARL, RAYMOND, 1915. Modes of research in genetics. The Macmillan Co., New York.

PEARL R., and MINER, J. R., 1914. A table for estimating the probable significance of statistical constants. Maine Agr. Exp. Sta., Bull. 226: 85–88.

PIPER, C. V., 1912. Agricultural varieties of the cowpea and immediately related species. U. S. Dept. Agr., Bur. Plant Indust., Bull. 229: 1–160.

1916. Forage plants and their culture. The Macmillan Co., New York, 618 pp.

PIPER, C. V. EVANS, M. W., MCKEE, R., and MORSE, W. J., 1914. Alfalfa seed production; pollination studies. U. S. Dept. Agr., Bull. 75, 32 pp.

PIPER, C. V. and MORSE, W. J., 1910. The soybean: History, varieties and field studies. U. S. Dept. Agr., Bur. Plant Indust., Bull. 197, 84 pp.

POWELL, G. H., 1898. Plant breeding. Am. Gard., **16**: 466–467, 514–515.

PRICE, H. L., and DRINKARD, A. W., JR., 1908. Inheritance in tomato hybrids. Virginia Agr. Exp. Sta., Bull. 177: 18–53.

1911–12. Inheritance in cabbage hybrids. Ann. Rept. Virginia Polytec. Inst. Agr. Exp. Sta. for **1911 and 1912**: 240–257.

PRIDHAM, J. T., 1916. Oat breeding experiments. Agr. Gaz. N. S. Wales, **27**: 457–461.

QUANJER, H. M., 1920. The mosaic disease of the Solanaceæ, its relation to the phloem-necrosis and its effect upon potato culture. Phytopath., **10**: 35–47.

REEVES, F. S., 1918. Report of Hort. Exp. Sta., Vineland, Ontario, for **1916–17**: 39–41.

RIOLLE, Y. T., 1914. Recherches morphologiques et biologiques sur les Radies cultives. Ann. Sci. Agron., **31st year**: 346–550.

ROBERTS, HERBERT F., 1919. The founders of the art of breeding. Jour. Heredity, **10**: 99–106, 147–152, 229–239, 257–275.

1919. The contribution of Carl Friedrich von Gärtner to the history of plant hybridization. Am. Nat., **53**: 431–445.

RÜMKER, K. VON, 1913. Ueber Roggenzüchtung. Btr. zur Pflanzenzücht., **3**: 8–28.

RÜMKER, K. VON, and LEIDNER, R., 1914. Ein Beitrag zur Frage der Inzucht bei Roggen. Zeitschr. für Pflanzenzücht., **2**: 427–444.

Russell, H. L., and Morrison, F. B., 1919. Service to Wisconsin. Wis. Agr. Exp. Sta., Bull. 302, 35 pp.

Sageret, A. 1826. Considerations sur la production des hybrides, des varietes et des varietes en general, et sur celles de la famille des Cucurbitacees en particulier. Ann. d. Sci. Nat., **8**: 294–314.

Salaman, R. N., 1910–11. The inheritance of color and other characters in the potato. Jour. Genetics, **1**: 7–46.

1912–13. A lecture on the hereditary characters in the potato. Jour. Roy. Hort. Soc., **38**: 34–39.

1909–11. Male sterility in potatoes, a dominant Mendelian character; with remarks on the shape of the pollen in wild and domestic varieties. Jour. Linnean Soc., **39**: 301–312.

1911 (1913). Studies in potato breeding. Int. Conf. de Genetique, **4**: 373–375.

Salmon, Cecil, 1914. Sterile florets in wheat and other cereals. Jour. Am. Soc. Agron., **6**: 24–30.

Saunders, C. E., 1905. A natural hybrid in wheat. Proc. Amer. Breeders' Assoc., **1**: 137–138.

1912. Marquis wheat. Exp. Farms' Rept., Ottawa, Canada, pp. 118–120.

Scott, W. B., 1917. The theory of evolution. The Macmillan Co., New York, 183 pp.

Setchell, W. A., 1912. Studies in Nicotiana. 1. Un v. Calif. Pub. in Bot., **5**: 1–86.

Shamel, A. D., and Cobey, W. W., 1907. Tobacco breeding. U. S. Dept. Agr., Bur. Plant Indust., Bull. 96, 71 pp.

1910. Tobacco breeding. Am. Breeders' Assoc. Rept., **6**: 268–275.

Shamel, A. D., Scott, L. B., and Pomeroy, C. S, 1918. Citrus-fruit improvement: A study of bud variation in the Washington navel orange. U. S. Dept. of Agr., Bull. 623, 146 pp.

1918. Citrus-fruit improvement: A study of bud variation in the Valencia orange. U. S. Dept. of Agr., Bull. 624, 120 pp.

1918. Citrus-fruit improvement: A study of bud variation in the Marsh grapefruit. U. S. Dept. of Agr., Bull. 697, 112 pp.

1919. Origin of a new and improved French prune variety. Jour. Heredity, 10: 339–343.

Shaw, H. B., 1916. Self-, close-, and cross-fertilization of beets. Mem. of N. Y. Bot. Gard., **6**: 149–152.

Shaw, J. K., and Norton, J. B., 1918. The inheritance of seed-coat color in garden beans. Massachusetts Agr. Exp. Sta., Bull. 185: 59–104.

Shull, G. H., 1908. The composition of a field of maize. Am. Breeders' Assoc. Rept., **4**: 296–301.

1909. A pure line method of corn breeding. Am. Breeders' Assoc. Rept., **5**: 51–59.

1915. Genetic definitions in the new standard dictionary. Amer. Nat., **59**: 52–59.

Smith, L. H., 1912. Occurrence of natural hybrids in wheat. Proc. Am. Breeders' Assoc., Rept. **7 & 8**: 412–414.

So, M., and Imal, Y., 1918. On the xenia of the barley. Bot. Mag., Tokyo, **32**: 205–214.

SPILLMAN, W. J., 1901. Quantitative studies in the transmission of parental characters to hybrid offspring. U. S. Dept. Agr., Office Exp. Sta., Bull. 115, 88–97.

1909. The hybrid wheats. Washington Agr. Exp. Sta., Bull. 89, 3–27.

1911.. Inheritance of the "eye" in Vigna. Am. Nat., **45**: 513–523.

1913. Color correlation in cowpeas. Science N. S., **38**: 302.

SPRAGG, F. A., 1919. Robust beans. Michigan Agr. Exp. Sta., Quart. Bull. 1: 173–174.

SPRAGG, F. A., and CLARK, A. J., 1916. Red Rock wheat. Michigan Agr. Exp. Sta. Cir. 31, 7 pp.

STAKMAN, E. C., HAYES, H. K., AAMODT, OLAF S., and LEACH, J. G., 1919. Controlling flax wilt by seed selection. Jour. Am. Soc. Agron., **11**: 291–298.

STAKMAN, E. C., LEVINE, M. N., and LEACH, J. G., 1919. New biologic forms of Puccinia graminis. Jour. Agr. Res., **16**: 103–105.

STEWART, F. C., 1916. Observations on some degenerate strains of potatoes. New York (Geneva) Agr. Exp. Sta., Bull. 422: 319–357.

STEWART, J. B., 1908. The production of cigar-wrapper tobacco under shade in the Connecticut Valley. U. S. Dept. Agr., Bur. Plant Indust., Bull. 138, 31 pp.

STEWART, J. P., 1912. Factors influencing yield, color, size, and growth in apples. Ann. Rept. Pennsylvania State College for **1910–11**: 401–492.

STOUT, A. B., 1915. The establishment of varieties in Coleus by the selection of somatic variations. Carnegie Inst. of Wash., Pub. 218: 1–80.

1920. Further exper mental studies on self-incompatibility in hermaphrodite plants. Jour. Genetics, **9**: 104.

STUART, WM., 1915. Potato breeding and selection. U. S. Dept. Agr., Bur. Plant Indust., Bull. 195, 35 pp.

STURTEVANT E. L., 1899. Varieties of corn. U. S. Dept. Agr., Office Exp. Sta., Bull. 57, 51–108.

SURFACE, F. M., 1916. Studies on oat breeding. III. On the inheritance of certain glume characters in the cross A. fatua × A. sativa, variety Kherson. Genetics, **1**: 252–286.

SURFACE, F. M., and ZINN, JACOB, 1916. Studies on oat breeding. IV. Pure line varieties. Main Agr. Exp. Sta., Bull. 250: 97–148.

SUTTON, A. W., 1908. Brassica crosses. Jour. of Linn. Soc., **38**: 337–349.

SUTTON, G. L., 1910. Varieties of wheat recommended by the Department of Agriculture. Agr. Gaz. of N. S. Wales, **21**: 185–193.

SUTTON, IDA, 1918. Report on tests of self-sterility in plums, cherries, and apples at the John Innes Horticultural Institution. Jour. Genetics, **7**: 281–300.

SWINGLE, W. T., 1913. Some new citrous fruits. Am. Breeders' Mag., **4**: 83–95.

TAMMES, TINE, 1911. Das Verhalten fluktuierend variierender Merkmale bei der Bastardierung. Rec. Trav. Bot. Neerl., **8**: 201–288.

1914. The explanation of an apparent exception to Mendel's law of segregation. Koninklyke Akademe van Wetenschappen. Te Amsterdam., **16**: 1021–1031.

1915. Die genotypische Zusammensetzung einiger Varietäten derselben Art und ihr genetischer Zusammenhang. Rec. Trav. Bot. Neerl., **12**: 217–277.

1916. Die gegenseitige Wirkung genotypischer Faktoren. Rec. Trav. Bot. Neerl. **13**: 44–62.

TERAO, H., 1918. Maternal inheritance in the soybean. Am. Nat., **52**: 51–56.

THATCHER, R. W., 1912. Dominant and recessive characters in barley and oat hybrids. Proc. Soc. Prom. Agr. Sci., **33**: 37–50.

THOMPSTONE, E., 1915. Some observations on upper Burma Paddy (grown under irrigation). Agr. Jour., India, **10**: 26–53.

TISDALE, W. H., 1916. Relation of soil temperature to infection of flax by Fusarium lini. Phytopath., **6**: 412–413.

1917. Flax wilt. A study of the nature and inheritance of wilt resistance. Jour. Agr. Res., **11**: 573–605.

TOWNSEND, C. O., 1909. Breeding sorghum. Am. Breeders' Assoc. Rept., **5**: 269–274.

TRABUT, L., 1914. The origin of cultivated oats. Jour. Heredity, **5**: 56–85.

TSCHERMAK, E. VON, 1901. Ueber Züchtung neuer Getreiderassen mittelst künstlicher Kreuzung. Zeitschr. f. d. Land. Versuch. in Oest., **4**: 1029–1060.

1906. Über Züchtung neuer Getreiderassen mittels künstlicher Kreuzung. II. Mitteilung. Kreuzungstudien am Roggen. Zeitschr. f. d. Landw. Versuch. in Oest., **9**: 699–743.

1913. Über seltene Getreidebastarde. Beiträge zur Pflanzenzücht., **3**: 49–61.

1914*a*. Die Verwertung der Bastardierung für phlogenetische Fragen in der Getreidegruppe. Zeitschr. für Pflanzenzücht., **2**: 303–304.

1914*b*. Über die Vererbungsweise von Art- und Gattungs-bastarden innerhalb der Getreidegruppe. Mitt. Landw. Lehrkanzeln K. K. Hochschule für Bodenkultur in Wien, **2**: 763–772.

1916. Über den gegenwärtigen Stand der Gemüsezüchtung. Zeitschr. für Pflanzenzücht., **4**: 65–104.

ULRICH, K., 1902. Die Bestäubung und Befruchtung des Roggens. Inaug. Diss. Halle.

VALLEAU, W. D., 1918. Sterility in the strawberry. Jour. Agr. Res., **12**: 613–669.

VILMORIN, LOUIS DE, 1852. Note sur la creation d'une nouvelle race de betterave a sucre., pp. 25–29. Notices sur L'Amerlioration des Plantes by Louis Lévéque de Vilmorin and André Lévéque de Vilmorin. Vilmorin-Andrieux, Paris.

VILMORIN, M. H., 1880. Essais de croisement entres bles differents. Bull. Soc. Bot. de France, **27**: 356–361.

1883. Exper ences de croisement entres des bles differents. Bull. Soc. Bot. de France, **30**: 58–63.

VILMORIN, P. DE, 1910. Recherches sur l'heredite mendelienne. In Compt. Rend. Acad. Sci., **151**: 548–551.

WAITE, M. B., 1905. Sterility in Japanese plums. Am. Agric., **75**: 112.

WALDRON, L. R., 1912. Hardiness in successive alfalfa generations. Am. Nat., **46**: 463–469.

1919. Cross-fertilization in alfalfa. Jour. Am. Soc. Agron., **11**: 259–266.

WALLER, A. E., 1917. A method for determining the percentage of self-pollination in maize. Jour. Am. Soc. Agron., **9**: 35–37.

WALTER, H. E., 1916. Genetics. The Macmillan Co., New York, 272 pp.

WARBURTON, C. W. 1914. Notes on oats for the Southern United States. Jour. Am. Soc. Agron., **6**: 118–121.

WAUGH, F. A., 1896. The pollination of plums. Vermont Agr. Exp. Sta., Bull. **53**: 47–65.

1897. Problems in plum-pollination. Vermont Agr. Exp. Sta. Ann. Rept., **10**: 87–98.

1898. Problems in plum-pollination. Vermont Agr. Exp. Sta. Ann. Rept., **11**: 238–262.

1899. The pollination of plums. Vermont Agr. Exp. Sta. Ann. Rept., **12**: 189–209.

1900. Further work in plum-pollination. Vermont Agr. Exp. Sta. Ann. Rept., **13**: 355–362.

1901. Plums and plum culture. Orange Judd Co., New York, 371 pp.

WEBBER, H. J., 1900. Xenia, or the immediate effect of pollen, in maize. U. S. Dept. Agr., Div. Veg. Phys. & Path., Bull. 22, 38 pp.

1905. Cotton breeding. In Am. Breeders' Assoc. Rept., **1**: 37–44.

1911. Preliminary notes on pepper hybrids. Amer. Breeders' Assoc. Rept., **8**: 188–199.

WEBBER, H. J., HUNT, T. F., GILMORE, J. W., CLARK, C. F., and FRASER, S., 1912. The production of new and improved varieties of timothy. New York Cornell Agr. Exp. Sta., Bull. 313: 339–392.

WEBBER, H. J. and ORTON, W. A., 1902. A cowpea resistant to root-knot. Part II. U. S. Dept. Agr., Bur. Plant Indust., Bull. 17, 23–36.

WELLINGTON, R., 1912. Influence of crossing in increasing the yield of the tomato. N. Y. Agr. Exp. Sta., Bull. 346: 57–76.

1913*a*. Studies of natural and artificial parthenogenesis in the genus Nicotiana. In Am. Nat., 47, 279–306.

1913*b*. Raspberry breeding. Soc. Hort. Sci. Rept. for **1913**: 155–159.

WESTGATE, J. M., 1910. Variegated alfalfa. U.S. Dept. Agr., Bur. Plant Indust., Bull. 169: 1–63.

1915. Red-clover seed production: pollination studies. U. S. Dept. of Agr., Bull. 289, 31 pp.

WHITE, O. E., 1910. Inheritance studies in Pisum. I. Inheritance of cotyledon color. Am. Nat., **50**: 530–547.

1916. The origin and history of our more common cultivated fruits. Brooklyn Bot. Gard. Leaflets, Series **4**: pp. 1–12.

1917. Inheritance of endosperm color in maize. Am. Jour. Botany, **4**: 396–406.

1917. Inheritance studies in Pisum. IV. Interrelation of the genetic factors of Pisum. Jour. Agr. Res., **11**: 167–190.

1918. Inheritance studies in Pisum. III. The inheritance of height in peas. Memoir of the Torrey Bot. Club, **17**: 316–322.

WIGHT, W. F., 1915. Native American species of prunes. U. S. Dept. of Agr., Bull. 179: 1–75.

1915. The varieties of plums derived from native American species. U. S. Dept. of Agri., Bull. 172: 1–44.

1916. Origin, introduction and primitive culture of the potato. Proc. Nat. Potato Assoc. of America, **3**: 35–52.

WILLIAMS, C. G., 1905. Pedigreed seed corn. Ohio Agr. Exp. Sta., Cir. 42: 1–11.

1907. Corn breeding and registration. Ohio Agr. Exp. Sta., Cir. 66: 1–14.

1916. Wheat experiments. Ohio Agr. Exp. Sta., Bull. 298: 449–484.

WILLIAMS, C. G. and WELTON, F. A., 1911. Wheat experiments. Ohio Agr. Exp. Sta., Bull. 231, 22 pp.

1913. Oats. Ohio Agr. Exp. Sta., Bull. 257: 255–283.

1915. Corn experiments. Ohio Agr. Exp. Sta., Bull. 282: 84–91.

WILSON, A. D., and WARBURTON, C. W., 1919. Field Crops. Webb Pub. Company, St. Paul, Minn., 509 pp.

WILSON, J. H., 1916. Further experiments in crossing potatoes. Trans. High. Agr. Soc. Scotland. Fifth series, **28**: 33–55.

WITTE, H., 1919. Breeding timothy at Svalöf. Jour. Heredity, **10**: 291–299.

WITTMACK, L., 1909. Studien über die Stammpflanzen der Kartoffel. Ber. Deutschen Bot. Gesell., **27**: 28–42.

WOOD, T. B., and STRATTON, F. J. M., 1910. The interpretation of experimental results. Jour. Agr. Sci., **3**: 417–440.

WOLFE, T. K., 1915. Further evidence of the immediate effect of crossing varieties of corn on the size of seed produced. Jour. Am. Soc. Agron., **7**: 265–272.

ZINN, JACOB, and SURFACE, F. M., 1917. Studies on oat breeding. V. The F_1 and F_2 generations of cross between a naked and a hulled oat. Jour. Agr. Res., **10**: 293–312.

INDEX

A

Aaronsohn, wild wheat, 78
Alfalfa, flower structure, 217
 Grimm variety, 216
 origin of, 215
 pollination in, 40, 207
 selection in, 293
 winter resistance, 218
Alkemine, rice pollination, 37
Allard, tobacco, inheritance in, 161
 tobacco mutations, 167
Apples, self-sterility in, 269, 271
 inheritance in, 271
Arny and Garber, weight of seed and plant vigor, 123
Arny and Hayes, border effect in plot tests, 61
Asparagus, pollination in, 253
 rust resistance, 253

B

Babcock and Clausen, crossing over, 27
 homozygosis following a cross, 117
 selection in sugar beets, 119
Backhouse, wheat species crosses, 79
 wheat-rye crosses, 106
Bailey, crosses in cucurbits, 256
 evolution in fruits, 264
 inheritance in raspberries, 272
 sweet corn, origin, 235
Bain and Essary, clover anthracnose, 215
Ball, pollination, grain sorghums, 38
Balls, cotton, natural crosses, 38, 173
 cotton, inheritance, 175
Barley, awn in relation to yield, 104
 classification, 98
Barley, independent Mendelian inheritance, 102
 inheritance of spike density, 28, 103
 pollination in, 36
 species crosses, 99
 winter *vs.* spring habit, 103
 xenia in, 103
Barrus, disease resistance in bean, 244
Beach, self-sterility in grape, 269
Beal, varietal crosses in maize, 202
Bean, classification, 241
 disease resistance in, 139, 244, 245
 flower structure, 243
 inheritance of characters, 242, 244
 M. A. C. Robust, 131
Beet, inheritance and breeding, 250
Belling, inheritance in velvet bean, 149
 varietal crosses, maize, 203
Biffin, barley inheritance, 102, 103
 disease resistance in wheat, 85, 134
 immediate effect of pollination in wheat, 82
 linkage in wheat crosses, 79
 polonicum-wheat crosses, 79
 species crosses, barley, 101
 wheat pollination, 35
Bolley, flax, wilt resistance, 157, 286
Brand, alfalfa, Grimm, 216
Brassica, inheritance studies in, 251
Breeding, asparagus, 254
 beets, 250
 by crossing, 116
 by selection, 115
 cabbage, 252
 clover, 215

Breeding, cotton, 177
cucurbits, 259
flax, 158
fruits, 266, 273, 278, 279
Hays, progeny test, 111
Hopkins, ear-to-row test, 111, 198
keeping records in, 111
maize, 196, 290
radish, 250
self-fertilized vegetables, 247
small grains, 111
soybeans, 148
timothy, Cornell station, 210, 211
at Svalöf, 212
wheat, 135, 137
Buckwheat, breeding, 108
characters of, 107
original home of, 107
species, 107
Bull, the Concord grape, 265
Burnett, oat selections, 131
Bushnell, squash, selfing in, 68
breeding, 260

C

Camerarius, on sexuality, 3
Caporn, inheritance, size characters oats, 96
Carleton, origin of rice, 108
Carrier, increase of seed size due to crossing, 201
Check plots, correcting yields by, 53, 55
estimating heterogeneity by, 53
in obtaining probable errors, 55
Cherries, self-sterility in, 269
Citranges, 277
Clover, pollination in, 207, 214
selection in, 292
species, 214
Coe, mutations in velvet beans, 150
Collins, origin of maize, 182
podded characters in maize, 189
varietal crosses in maize, 202, 203
Collins and Kempton, endosperm characters in maize, 185
Collins and Kempton, increase in seed size due to a cross, 201
Competition in variety test, 63
in rod row tests, 64
Correlations, morphological characters and lodging, small grains, 127
value of, 125
Correns, endosperm characters of maize, 185
xenia in maize, 183
Cotton, chromosome number, 177
cultivated species, 173
disease resistance, 177, 178
flower structure, 174, 175
inheritance in, 176
mutations in, 177
natural crosses in, 38, 173
origin of, 173
Cowpea, inheritance in, 143, 144
Iron, a variety of, 131
origin, 143
resistance to disease, 144, 145
selection and crossing results, 145
Crane, inheritance in tomato, 245
Crop improvement, value of, 14, 15
Crops, mode of reproduction of, 33, 34
Crosses, handling of, 116
Crossing, artificial, 68
small grains, 69
technic of, 74
Crossing-over, 12, 27
Cucumber, heterosis in, 257
inheritance, 257
Cucurbit crosses, 7
classification, 255
Cytology, reduction division in plants, 17, 18

D

Darwin, heredity, 10
natural selection, 9
variability, 10
Date palm, sexuality, 3
De Candolle, origin and antiquity of vegetables, 235

Dillman, selection in sorghum, 179
Disease resistance, in asparagus, 253
in beans, 139, 244
in cabbage, 252
in clover, 215
in cotton, 177
in cowpeas, 144, 145
in flax, 151
in oats, 95
in rice, 109
in timothy, 213
in tomatoes, 248
in watermelons, 258
in wheat, 76, 85, 134
Dorsey, breeding fruits, 279
mutations in fruits, 264
origin of fruits, 263
self-fertile and self-sterile fruits, 269
self-sterility in grape, plum, 270
Durst, disease resistant tomatoes, 248

E

East, artificial crossing, 68
maize, ear-to-row tests, 198
self-fertilization in, 202
mathematical requirements of size inheritance, 163, 164
potato, clonal selection, 228
introduction to Europe, 220
pollination in, 224, 225
species in, 219
tobacco, color of flowers, 161
size of flower, 165
species crosses, 159
sterility in, 160
East and Hayes, hybrid vigor, 45, 47
maize, inheritance, 185, 187
pericarp color, 188
podded character, 189
seed and ear characters, 192
subspecies of, 182
East and Jones, factor stability, 32
loss mutations, 276
size inheritance, 30
East and Park, sterility in tobacco, 160
Edgerton, disease resistance in tomatoes, 248
Emerson, bean, inheritance in, 242
maize, auricle and ligule, 189
cob color, 188
endosperm characters, 187
squash, size inheritance in, 258
tomato, inheritance, 246
Emerson and East, size inheritance, 192
Engledow, linkage in wheat crosses, 79
Etheridge, oat classification, 89

F

Failyer and Willard, selection in sorghum, 179
Farrar, wheat breeding, 135
Fertilization, maize, 19
Field plot technic, 65, 266
Flax, breeding, 158
flower structure, 154
inheritance, 155, 156
natural crosses, 37
origin of, 153
species crosses, 153
wilt resistance, 158, 287
Fletcher, self-sterility in pears, 269
strawberry, varieties, 262
Focke, xenia, 183
Frear, crossing in uncovered wheat spikes, 69
Freeman, linkage in wheat, 80
seed characters of wheat, 82
sterility in wheat crosses, 79
Fruits, crosses in, 277
early breeders of, 264
origin, antiquity of, 261, 264
self-sterility and heterozygosity in, 267
Fruwirth, barley pollination, 36
flax, natural crosses, 37
maize, self-fertilization, 39
oats, natural crosses, 36
potatoes, inheritance in, 221
pure-line selection, 12
rye, pollination in, 40
wheat, pollination, 35
winter-spring habit, barley, 103

G

Gaines, disease resistance in wheat, 86
oat crosses, 93
seed characters in wheat, 82
spike density in wheat, 81
Gametes, production in flowering plants, 17
Garber, stem rust in oats, 95
Garber and Olson, stem characters of small grains, 127
Garner, tobacco mutations, 167
Garner and Allard, effect of length of day on flowering, 169
Genetics, factor stability, 32
inheritance factors, 20
inheritance, two independently inherited factors, 23
linkage, 26
method of studying, 16
size characters, 27
Germ plasm, constancy of, 10
Gilbert, potato characters, 223
Giltay, xenia in rye, 106
Goff, self-sterility in plum, 269
Goodspeed, parthenogenesis in tobacco, 160
size inheritance in tobacco, 165
Goss, early pea crosses, 7
Graham, inheritance in sorghum, 179
pollination of sorghum, 38
Grape, early breeding, 265
inheritance in, 272
self-sterility in, 269
Grasses, pollination in, 41, 207
economic species, 207
selection in, 293
Griffee, F_1 wheat crosses, 43
Groth, inheritance in tomato, 245
Guignard, double fertilization, 183

H

Hagedoorn, early wheat selections, 119
Hallet, early selections in small grains, 118
Hansen, fruit breeding, 278
Harlan, barley, natural crosses, 36
classification of barley, 98
Harlan and Anthony, the barley awn, 104
Harlan and Hayes, barley species crosses, 99
Harland, cowpea, inheritance, 143, 144
natural crosses, 39
Harris, soil heterogeneity, 51
Harshberger, home of maize, 181
Hartley and others, varietal crosses of maize, 203
Hasselbring, pure lines in tobacco, 166
Hayes, maize, self-pollination, 39
pericarp color, maize, 188
pure-line selection, tobacco, 122, 166
size characters, 165
tobacco mutations, 167
Hayes and Arny, replication, 59
Hayes and Beinhart, tobacco mutations, 167
Hayes and East, maize inheritance, 185, 192
maize, varietal crosses, 203
Hayes, East and Beinhart, size characters, tobacco, 162, 165
Hayes and Garber, winter hardiness in wheat, 87, 138
high protein maize, 195
Hayes and Harlan, barley, spike density, 104
Hayes and Jones, F_1 tomato crosses, 43
Hayes and Olson, F_1 varietal maize crosses, 203
Hayes and others, disease resistance in wheat, 85
sterility in wheat, 79
Hayes and Stakman, rust in timothy, 213
Hays, small grain breeding, 112
Head thrasher, small grains, 117
Heckel, mutations in potatoes, 220
Hector, inheritance in rice, 109
natural crosses in rice, 37

Hedrick and Anthony, inheritance in grape and raspberry, 272
Hedrick and Wellington, inheritance in apples, 268, 271
Henkemeyer, chaff characters in wheat, 84
Heterogeneity, in field plots, 51
estimating, 53
inheritance in raspberry, 272
Hildebrand, rye pollination, 39
Hilson, inheritance in sorghum, 178
Homozygosis, from self-fertilization, 49
Hopkins, ear-to-row maize, 198
Hoshino, inheritance in rice, 109, 110
Houser, F_1 tobacco crosses, 42
Howard and others, inheritance, beards in wheat, 85
chaff characters in wheat, 84
seed characters in wheat, 82
standing power in wheat, 88
natural crosses, in beans and peas, 39
flax, 37
tobacco, 36
wheat, 35
parthenogenesis in tobacco, 160
tobacco groups, 159
Hutcheson, pure-line selection, 122
Hutcheson and Wolf, maize varietal crosses, 203
Hybrid vigor, 47

I

Ikeno, inheritance, in rice, 108, 109
inheritance, in peppers, 247
natural crosses in rice, 37

J

Jardine, Kanred wheat, 76, 128
Jellneck, artificial wheat crosses, 71
Jenkins, number of seeds per tobacco plant, 36
Jensen, plant height, tobacco, 165
Jesenko, wheat-rye crosses, 106
Johannsen, the pure line, 11, 120
Johnson, cytology of fertilization, 5
sex in date palm, 3
tobacco breeding, 140
tobacco inheritance, 165
Jones, crossing selfed strains, maize, 205
heterosis, 49
homozygosis on selfing, 49
increased seed size in a cross, 201
inheritance, pseudo-starchy, maize, 184
lethal endosperm, maize, 185
tomato, 246
self-fertilization, maize, 47
Jones and Gallastegui, podded character, maize, 189
Jones and Gilman, disease resistance, cabbage, 252
self-sterility, cabbage, 251
Jones and others, varietal crosses, maize, 203

K

Kajanus, inheritance in beet, 250
Karper and Conner, pollination, grain sorghums, 38
Kearney, cotton mutations, 177
Keeble and Pellew, inheritance in pea, 236
Kezer and Boyack, wheat crosses, 79, 80
Kiesselbach, competition in variety tests, 63
ear-to-row breeding, maize, 199
varietal crosses, maize, 203
Kiesselbach and Ratcliff, selection in oats, 130
Kirchner, wheat pollination, 35
Knight, early crosses, 6
fruit breeding, 264
self-sterility in apple, 271
Knuth, maize pollination, 39
Koch, inheritance in rice, 109, 110
Koelreuter, early crosses, 5

L

Leake, cotton inheritance, 175
cotton, natural crosses, 38

Le Couteur, selection, small grains, 119
Legumes, crossing artificially, 72
Leidigh, self-fertilizing sorghums, 180
Leighty, wheat-rye crosses, 35, 106
Leighty and Hutcheson, blooming in wheat, 35, 69
Lewis and Vincent, heterosis in apples, 269
self-sterility in apples, 269
Lily, anther and pollen of, 18
Lindstrom, chlorophyll inheritance, maize, 190
Linkage, in cotton, 175
in oats, 97
in pea, 241
in tomato, 246
in wheat, 79, 80, 84
of characters, 26
Love and Craig, pure-line selections, oats, 123
chaff characters, wheat, 84
oat crosses, 92, 93, 94
rod-row method, 114
thrashing machine, 117
wheat, species crosses, 78
wheat-rye crosses, 106
Love and McRostie, hulled *vs.* hull-less, oats, 93
Lumsden, inheritance in muskmelon, 257

M

MacDougal, inheritance in potatoes, 222
Macoun, degeneracy in potato, 230
hardy fruits, 277
Maize, chemical composition, 193
chlorophyll inheritance, 190
ear characters and yield, 197
ear-to-row breeding, 198
effects of self-fertilization, 46, 47
endosperm character inheritance, 185
fertilization in, 19
heterosis in, 200
home grown seed, 199
Maize, increase in seed size from crossing, 201
near relatives of, 181
origin of, 182
plant character inheritance, 187–196
podded condition of, 189
Malte and Macoun, crossing in vegetables, 251
Martin, clover, pollen germination, 215
Mayer-Gmelin, spike density in wheat, 81
McFadden, wheat-rye crosses, 106
McRostie, beans, disease resistance, 139, 245
Mendel's law, 12
Mercer and Hall, replication in plot test, 59
size and shape of plot, 60, 61
Montgomery, ear-to-row maize, 198
origin of maize, 181
rod-row method, 115
size of plot, 60
weight of seed planted, 126
Morrow and Gardner, varietal crosses, maize, 202, 203
Munson, evolution of fruits, 264
Muskmelon, inheritance in, 257
Mutations, cotton, 177
due to loss of factors, 276
fruits, 273
maize, 189
potatoes, 220, 229
tobacco, 167
velvet beans, 150

N

Nabours, cross-overs in parthenogenesis, 276
Natural selection, 9
Naudin, on segregation, 7
on cucurbit classification, 254
Nawaschin, double fertilization, 183
New introductions, 113
Newman, correlations, 125
improvement by crossing, 134
selection methods, 127

Nilsson, inheritance in potatoes, 221
oat, classification, 95
potato, degeneracy in, 232
rye, self-pollination, 40
Nilsson-Ehle, oat inheritance, 92, 93, 95, 96, 97, 133
oats, false wild, 97
wheat, disease resistance, 85
seed characters in, 82
spike density in, 81
winter-hardiness, 87
Norton, *A. sterilis*, oats, 90
rust resistance, asparagus, 254
time of blooming, oats, 71

O

Oats, awn development, 90
color of lemma, 93
color of stem, 92
disease resistance, 95
false wild, 97
improvement by crossing, 133
linkage in, 97
natural crosses, 36
open *vs.* side panicle, 95
origin of, 90
pubescence on grain, 94
selection in, 129, 130, 131
size characters, 96
species groups, 89
yellow factor, 92
Oliver, crossing methods, 71
Olson, Bull and Hayes, ear characters and yield, maize, 198
Origin and development of crops, 1
Orton, cotton, wilt resistance, 177
cowpea, resistance and wilt and root-knot, 144
watermelon, wilt resistance, 258

P

Pammel, crosses in cucurbits, 256
Parker, disease resistance in oats, 95
spike density in wheat, 81
Parnell and others, inheritance in rice, 109
natural crosses in rice, 37
Pea, classification of, 236
genetic factors in, 240
inheritance in, 236
linkage in, 241
natural crosses, 38
structure of flower, 237
Pear, self-sterility in, 269
Pearl and Miner, probable errors, 56
Pepper, characters, 246
inheritance in, 247
Piper, alfalfa, origin and species, 215
cowpea, breeding, 146
cowpea, origin of, 143
pea, natural crosses, 38
sorghum species, 178
soybeans, natural crosses, 39
Piper and Morse, origin of soybean, 146
Piper and others, alfalfa pollination, 40, 216
Plant breeding, development of art, 2
relation of biological principles to, 8
Plum, self-sterility in, 269
Pollination, artificial crosses, oats, 71
artificial self-pollination, 67
depollination with water, 73
tools for, 73
Pope, pollination of crop plants, 34
Price, cabbage, self-sterility, 251
inheritance in cabbage, 251
Price and Drinkard, tomato inheritance, 245
Pridham, oat crosses, 36, 93
Probable error, use of, 56
in eliminating strains, 57
pairing method of obtaining, 57
Pure line theory, 11, 120, 121

Q

Quanjer, diseases in potatoes, 231

R

Radish, origin, inheritance, breeding, 249
Raspberry, inheritance, 272

Ray, species, first use of term, 9
Replication, value of, 58
correct method of, 60
reducing probable error by, 59
Rice, important characters of, 108
inheritance summary, 109
natural crosses, 37
origin, 108
Rimpau, barley pollination, 36
oat crosses, 36
Riolle, radish inheritance, 249
Roberts, on early plant breeders, 5–8
Roguing, seed plots, 180
Rümker, von, xenia in rye, 106
inheritance in rye, 106
Russell and Morrison, natural crosses, soybean, 39
Rye, pollination, 39, 106
winter *vs.* spring, 106
xenia in, 106

S

Salaman, potato inheritance, 221
Salmon, blooming in wheat, 69
Sargaret, cucurbits, classification, 254
cucurbits, crosses in, 7
Saunders, Marquis wheat, 136
wheat crosses, 36
Scott, evolution, 8
Seed, improved corn, 287
pure bred, 281
registered, 286, 293
what is good, 282
wilt resistant flax, 287
Selection, individual plant, 119, 128
in small grains, early workers, 118, 119
isolation of pure lines, 125
methods of, 114, 115
sorghum, sugar content, 179
Self-fertilization, in normally cross-fertilized species, 45, 205
Setchell, tobacco sections, 159
Sexuality, Camerarius proves fact, 3
further proof of, 4
Shamel, tobacco breeding, 165
Shamel and Cobey, tobacco breeding, 166
Shamel and others, bud selection in fruits, 274
Shaw, self-fertilization in beet, 250
Shaw and Norton, inheritance in beans, 242
Shirreff, early selections, 118
Shull, self-fertilization in maize, 202, 205
Smith, selection for chemical content, maize, 193
Sorghum, breeding, 179
classification, 178
inheritance in, 178
origin of, 178
self-fertilization in, 38, 180
Soybeans, breeding, 148
characters of, 146
inheritance in, 147
natural crosses, 39
origin of, 146
Species, crosses, F_1, tobacco, 45
crosses, willow, 8
first use of term, 9
Spillman, cowpea inheritance, 143, 144
wheat, density of spike, 81
Spragg, M. A. C. Robust bean, 131
Spragg and Clark, Red Rock wheat, 128
Squash, breeding, 259
flower structure, 255
size inheritance, 258
Stakman and others, biologic forms of rust, 85
flax wilt resistance, 157
Stewart, bud selection in fruits, 275
tobacco breeding, 166
Stout, bud variations, 274, 276
Stuart, potato breeding, 223, 224, 226
Surface, oat inheritance, 92, 93
oat selections, 129
oat species crosses, 90, 94
Sutton, Brassica crosses, 251
self-sterility, fruits, 269
Swingle, citrus fruits, 277

T

Tammes, flax inheritance, 155, 156
flax species crosses, 153
Thatcher, barley inheritance, 102
Thompstone, inheritance in rice, 109
natural crosses in rice, 37
Timothy, breeding, 210
flower structure, 209
variability in, 208
Tisdale, flax wilt, inheritance, 158
Tobacco, breeding, 140
classification in groups, 159
color of flowers, inheritance, 161
F_1 crosses, vigor of, 42
mutations in, 167
natural crosses in, 36
number of seeds per plant, 36
parthenogenesis in, 160
quantitative characters, inheritance, 162
Tolaas and Bisby, disease-free potatoes, 291
Tomato, characters of, 245
F_1 crosses, vigor of, 42, 43
inheritance, 245, 246
natural crosses, 39
Townsend, self-fertilization in sorghum, 180
Trabut, oats, *A. sterilis* origin, 90
Tschermak, barley inheritance, 102
bean inheritance, 242
oats, natural crosses, 36
oats, species crosses, 90
pea, inheritance, 238, 239
rye, wild rye, 106
rye, winter *vs.* spring habit, 106
tomato, inheritance, 245
vegetable, mass selection, 250
wheat, species groups and crosses, 77, 78

U

Ulrich, rye-pollination, 40

V

Valleau, sterility in strawberry, 270
Variations, hybridization, 13
Variations, mutations, 21
new combination, 21
non-heritable, 20
Vegetables, cross-fertilized group, 248
origin and antiquity of, 235
self-fertilized group, 234
Velvet bean, breeding, 151
characters and inheritance, 149
mutations in, 150
origin, 149
Vilmorin, early selections, 119
selection in beets, 250
wheat species crosses, 77
Von Mons, selection in fruits, 264
DeVries, correlations, value of, 125
individual plant method of selection, 120
wheat, barley and oats pollination, 35
xenia in maize, 183

W

Waite, self-sterility in plum, 269
Waldron, alfalfa, natural crosses, 40
pollination of, 216
winter hardiness, 216
Waller, normal self-pollination in maize, 39
Watermelon, wilt resistance in, 258
Waugh, self-sterility in plum, 269
Webber, cotton inheritance, 177
cotton, natural crosses, 38, 173
pepper inheritance, 247
timothy breeding, 210
xenia in maize, 183
Webber and Orton, cowpea, disease resistance, 145
Weigmann, early crosses, 5
Weissmann, constancy of germ plasm, 10
Wellington, F_1 tomato crosses, 42
heterosis and inheritance, cucumber, 257
parthenogenesis in tobacco, 160
raspberry inheritance, 272
Westgate and others, clover, seed setting, 214

Wheat, artificial crossing of, 69, 71
awns in wheat, 85
blooming in, 69
breeding, 134, 135
chaff characters, 84
classification of species, 77
disease resistance, 85, 87, 134
F_1 crosses, vigor, 43–45
flower structure, 34, 70
hardiness in, 87
improvement by crossing, 134
Kanred, 76, 128
linkage in crosses, 79, 80, 84
Marquis, 136
natural crosses in, 34–36
Polonicum crosses, 79
Red Rock, 128
seed characters, 81–84
size characters, 88
species crosses, 77, 78
spike density, 81
sterility in species crosses, 79
T. dicoccoides, wild, 78
wheat-rye crosses, 35, 106
White, endosperm characters, maize, 186
fruit, origin, and antiquity of, 261
inheritance in pea, 236, 239, 240
Wichura, species crosses, willow, 8
Wight, potato species, 219
plum species, 262, 265
Williams, ear-to-row, maize, 198
selection for stiff straw, wheat, 129
Williams and Welton, ear characters and yield, maize, 197
varietal crosses, maize, 203
weight of seed planted and yield, 124
Wilson, inheritance, potatoes, 222
Wilson and Warburton, cotton species, 175
Witte, timothy breeding, 212
Wittmack, origin of potatoes, 220
Wolf, seed size increase due to cross, maize, 201
Wood and Stratton, checks in correcting yield, 53
probable error by pairing method, 58

X

Xenia in barley, 103
in maize, 183
in rice, 37
in rye, 106
law in maize, 184

164605 Bot. H.

Author Hayes, Herbert Kendall and Garber, Ralph John

Title Breeding crop plants.

DATE

NAME OF

University of Toronto Library

DO NOT REMOVE THE CARD FROM THIS POCKET

Acme Library Card Pocket
Under Pat. "Ref. Index File"
Made by LIBRARY BUREAU